In compliance with the
Canadian Privacy Legislation
some supporting forms
may have been removed from
this dissertation.

While these forms may be included
in the document page count,
their removal does not represent
any loss of content from the dissertation.

**University of Alberta**

# Tropical Dry and Tropical Moist Forest Characterization Through Remote Sensing

by

Margaret Erika Rose Kalácska

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the
degree of Master of Science

Department of Earth and Atmospheric Sciences

Edmonton, Alberta
Fall 2003

National Library of Canada
Acquisitions and Bibliographic Services
395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale du Canada
Acquisisitons et services bibliographiques
395, rue Wellington
Ottawa ON K1A 0N4
Canada

*Your file Votre référence*
*ISBN: 0-612-87794-9*
*Our file Notre référence*
*ISBN: 0-612-87794-9*

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou aturement reproduits sans son autorisation.

Canada

**University of Alberta**

**Library Release Form**

**Name of Author:** Margaret Erika Rose Kalácska

**Title of Thesis:** Tropical Dry and Tropical Moist Forest Characterization Through Remote Sensing

**Degree:** Master of Science

**Year this Degree Granted:** 2003

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.

Date: Aug. 10 2003

**University of Alberta**

**Faculty of Graduate Studies and Research**

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Tropical Dry and Tropical Moist Forest Characterization Through Remote Sensing* submitted by *Margaret Erika Rose Kalácska* in partial fulfillment of the requirements for the degree of Master of Science.

Dr. G. Arturo Sánchez-Azofeifa
(Supervisor)
Earth and Atmospheric Sciences Department

Dr. Benoit Rivard
Earth and Atmospheric Sciences Department

Dr. Terry Caelli
Computing Science Department

Date: August 9, 2003

**ABSTRACT**

The causes of phenological change and their implications for conservation biology and land use / cover change was reviewed with regards to remote sensing studies. In addition, an analysis of the relationship between leaf area index (LAI) and five spectral vegetation indices (SVI) was carried out in a Tropical Moist Forest (*T-mf*) environment. It was found that a Lorentzian Cumulative Function best fit the data and provided parameter estimation for the range of LAI values to which each index was sensitive to in this environment. In addition, a robust parametric linear regression was compared to a classical least-squares regression for the same LAI-SVI relationships. Finally, the floristic diversity and composition of a Tropical Dry Forest (*T-df*) along with LAI was examined in three successional stages. The stages were found to be asynchronous through the seasonal leaf cycle with the intermediate stage being the most different. The LAI measurements study area (Santa Rosa National Park, Costa Rica) were compared in an ongoing study with results from another nearby *T-df* in the Palo Verde National Park, Costa Rica.

**ACKNOWLEDGEMENTS**

I would like to extend a special appreciation and acknowledgement to my supervisor, Dr. Arturo Sánchez-Azofeifa for his support, dedication, generosity and encouragement making it possible for me to realize this project and my academic goals.

I also extend my appreciation to Dr. Benoit Rivard for his patience and support throughout the entire project. I give special thanks to Drs. Terry Caelli and Ron Hall for their time and help in all phases of this project.

I am sincerely grateful to Dr. Julio Calvo for his unconditional support, mentorship and total dedication, making it possible for me to reach my academic goals. I would also like to thank the following people for their guidance and assistance: Drs. Mauricio Quesada, Kathryn Stoner, Eugenio González, Daniel Janzen, Marco Gutierrez, Alan Journet and Mr. Ken Dutchak.

I would like to recognize the help of my colleagues and friends Pablo Arroyo-Mora, Roger Bonilla, Karen Castro, Manuel Castro, Luis Coronado-Chacón, Árpád Csányi, Tomas de Camino-Beck, Sheri Foley, Stewart Gill, Ericka Gongóra-Brenes, Steven Hamilton, Mark Kachmar, Steven Kembel, Wagner López-Vargas, April Mitchell, Evelyn Ramirez, Seth Rattet, Shasta Rudyk, Juan Carlos Solano, Patrick van Laake, Jason Young and Jinkai Zhang without whose help this project would not have been possible. I would also like to thank my parents Gábor and Erika Kalácska and uncle Andrew Kalácska for their unconditional support throughout all these years

I would like to extend my gratitude to Drs. Dick Peter Colleen Cassidy St.-Clair for assisting me in participating in the Tropical Biology: An Ecological Approach field course in Costa Rica from the Organization for Tropical Studies. A sincere thank you to

Drs. Deedra McClearn and Jim Hunt the co-coordinators of the course for their encouragement.

I extend a sincere appreciation to Jaime Viquez, Denis Ortiz-Ortiz, Patricia Murillo, Roberto Espinoza, Ulises Chavarria, Nelson Zamora and Vicente Watson for their assistance.

Special thanks to Lori Constantine from FSIDA, Grazyna Beudoin from CIDA-CBIE and Sally McLean from DFAIT for their support. I would also like to thank Roger Blanco, Maria Marta, Magdalena Rodriguez and Waldy Medina from Santa Rosa National Park and Jose Antonio Guzmán, Mauricio Solis and Mauricio Castillo from Palo Verde National Park.

A sincere thank you for financial support for the realization of this project to the University of Albert Fund for Support for International Development Activities (FSIDA), the Canadian International Development Agency (CIDA - CBIE), the National Geographic Society, the Tinker Foundation, the US National Science Foundation, the Canadian Development Agency, the Inter-American Institute, Palo Verde National Park and the University of Alberta Faculty of Science.

## TABLE OF CONTENTS

**Chapter 1 – Introduction** ..... 1

**Chapter 2 – "Tropical Dry Climates"**

2.1 – Introduction ..... 11
2.2 – Causes of Phenological Change ..... 14
2.3 – Conservation Biology ..... 17
2.4 – Phenology and Land Use / Cover Change ..... 21
2.5 – Final Remarks ..... 25
2.6 – References ..... 27

**Chapter 3 – "Leaf Area Index Measurements in a Tropical Moist Forest: A Case Study from Costa Rica"**

3.1 – Introduction ..... 43
3.2 – Methods ..... 48
3.3 – Results ..... 56
3.4 – Discussion ..... 62
3.5 – Conclusions ..... 68
3.6 – References ..... 69

**Chapter 4 – "Species composition, similarity, diversity and leaf area index from a Costa Rican Tropical Dry Forest"**

4.1 – Introduction ..... 102
4.2 – Methods ..... 104
4.3 – Results ..... 113
4.4 – Discussion ..... 118
4.5 – Conclusions ..... 124
4.6 – References ..... 124
Appendix I ..... 132

**Appendix A – Comparison of leaf area index between Santa Rosa and Palo Verde National Parks – a continuing analysis**

A.1 – Introduction ..... 158
A.2 – Results ..... 159
A.3 – Discussion ..... 159

## LIST OF TABLES

Table 3.1 Formulas for the five vegetation indices used in the analysis ..... 78

Table 3.2 List of species inventoried in sample plots at Los Inocentes..... 79

Table 3.3 Mean values of the forest structural characteristics..... 81

Table 3.4 Summary statistics for LAI in the different successional stages ..... 82

Table 3.5 Parameters of the best – Lorentzian Cumulative models for the LAI-SVI relationships..... 83

Table 3.6 Formulas for the propagation of errors through the vegetation indices derived from the standard rule of error propagation in arithmetic operations..... 84

Table 3.7 Mean SVI values and total error values for each vegetation index calculated from the formulas in Table 3.6 ..... 85

Table 3.8 Best-fit Theil-Sen and linear Least squares models with adjusted $R^2$ ..... 86

Table 4.1 Dates of LAI collection, Santa Rosa National Park..... 133

Table 4.2 List of woody species identified in the three successional stages in Santa Rosa National Park..... 134

Table 4.3 Families with a % composition greater than 5% in the three stages..... 138

Table 4.4 Brillouin and Shannon diversity indices along with their respective measures of evenness..... 139

Table 4.5 Morista-Horn and Sørenson similarity measures..... 140

Table 4.6 Mean values of forest structural characteristics..... 141

Table 4.7 Maximum and minimum LAI values for each plot along with ratio of the possible contribution of WAI..... 142

Table 4.8 Land use and anthropogenic fire history of the sites with the greatest similarity in species composition ..... 143

Table A.1 Mean, standard deviation and D'Agostino-Pearson test for departure from normality P values of optical estimates of LAI in Palo Verde and Santa Rosa National Parks ..... 162

## LIST OF FIGURES

Figure 1.1 The American Tropics, bordered by the Tropics of Cancer and Capricorn ..... 8

Figure 1.2 a) Chorotega Region in Cost Rica b) Life zones supported by the Chorotega region ..... 9

Figure 1.3 Areas around the world with a favourable climate for supporting Tropical dry and Tropical moist forests ..... 10

Figure 2.1 Areas around the world with a climate favourable for supporting a dry forest ecosystem ..... 40

Figure 2.2 Climate diagrams for fourteen representative sites in Costa Rica and Chamela, Mexico ..... 41

Figure 2.3. Spectral signatures of the dry forest at the Santa Rosa National Park from Landsat TM 5 images. a) wet season (October) and b) dry season (April) ..... 42

Figure 3.1 a) Los Inocentes in the Province of Guanacaste, Northwestern Costa Rica b) Quickbird multispectral image of the Los Inocentes property ..... 87

Figure 3.2 Ripley's K function for a spatial point pattern ..... 89

Figure 3.3 Climate diagram for Los Inocentes ..... 90

Figure 3.4 Idealized profiles for the four successional stages ..... 91

Figure 3.5 Leaf area index of each successional stage ..... 92

Figure 3.6 Frequency distribution and probability density functions of LAI in the different stages ..... 93

Figure 3.7 Red and near infrared reflectance per successional stage ..... 95

Figure 3.8 LAI vs. the five vegetation indices a) NDVI b) NLI c) SR d) MSR

e) SAVI2 ..... 96

Figure 3.9 Best-fit non-linear function – Lorentzian Cumulative function

a) SAVI2 b) MSR c) NDVI d) NLI e) SR ..... 98

Figure 3.10 Comparison of least-squares and Theil-Sen linear regressions ..... 100

Figure 4.1 Locations of early, intermediate and late plots in Santa Rosa

National Park ..... 144

Figure 4.2 Climate diagram for Santa Rosa National Park ..... 145

Figure 4.3 Examples of successional stage from Quickbird images with

LAI sampling scheme superimposed ..... 146

Figure 4.4 Ripley's K function for a spatial point pattern ..... 147

Figure 4.5 Agglomerative hierarchical cluster analysis of species composition ... 148

Figure 4.6 Fuzzy partitioning of structural variables ..... 149

Figure 4.7 Box plots for LAI in the dry and wet seasons ..... 150

Figure 4.8 Contour plots of LAI for the three stages ..... 151

Figure 4.9 Fourth order polynomial fitted to the LAI of the three stages through

the seasons ..... 153

Figure 4.10 Weight and number of species collected from litter trap data ..... 155

Figure 4.11 Simple Bayesian Network for seasonal LAI data ..... 157

Figure A.1 Plots located in Palo Verde National Park ..... 163

Figure A.2 Climate diagram of Palo Verde National Park ..... 164

Figure A.3 Ripley's K function for a spatial point pattern ..... 165

Figure A.4 Optical LAI estimations from April 2003 for Palo Verde and Santa

Rosa National Parks ..... 166

## 1.1 Introduction

In the American Tropics (Mexico to Southern rim of the Amazon Basin) (Figure 1.1), the vegetation has changed dramatically through time due to both natural and anthropogenic forces. In the Mesoamerican region (Mexico to Panama) over the course of the final 12,000 years of the last glacial cycle (22,000 – 10,000 B.P.) a decrease of 5 – 7°C in temperature and 25 – 40% in precipitation induced a replacement of the lowland rain forests by drier forests (Piperno and Pearsall 2000). In addition, areas with seasonal forests were replaced by vegetation similar to modern thorn woodland. Piperno and Pearsall (2000) reconstructed the vegetation of the lowland tropics for the period of 20,000 - 10,500 B.P. Their findings indicate during that time period the Chorotega Region in Costa Rica, the region encompassing the study area, (Figure 1.2a) was dominated by open vegetation such as undifferentiated woodland, low scrub and wooded savannah vegetation. Since the end of the last glacial period, the climate has changed and in this age, the Chorotega region is composed of areas with a climate capable of supporting eight different life zones (Figure 1.2b). All of these classifications are based on the World Life Zone System from Holdridge (1967).

Particularly threatened from LUCC (land use cover change) forces have been the Tropical Dry forest (*T-df)* and Tropical Moist Forest (*T-mf)* ecosystems. Worldwide, 42% of the tropical forests are *T-df* and 33% are *T-mf* (Holdridge 1967) (Figure 1.3). In these two areas, environmental and biotic stresses are the lowest compared to other tropical life zones (Ewel 1999). Other life zones are too cold, dry or wet. Therefore, the *T-df* and *T-mf* have been the preferred zones for

agriculture and human settlement. In Central America, 79% of the population in lives in these two life zones (Murphy and Lugo 1986). In addition, in the American Tropics, 19 of the 20 capitals are located in the *T-df* or *T-mf* (Holdridge 1967). Various political and economic factors have increased anthropogenic stresses in these two ecosystems leading to severe disturbances and widespread clearing (Sanchez-Azofeifa 1996).

Subsequent changes in global markets and economic consequences of the extensive deforestation caused revisions to public policies and land management practices leading to a stabilizing of Costa Rica's forest cover (Sanchez-Azofeifa et al. 2002) and in certain areas (ex. Chorotega) even a regeneration (Arroyo-Mora 2002). In addition to that, with a recent rise in public concern over global climate change, tropical forests have come to be considered as a possible carbon sink to offset carbon emissions (Pfaff et al. 2000). However, in order for any economic projection to be legitimate, accurate LUCC data needs to be gathered. And for that, large-scale monitoring systems need to be developed.

Monitoring tropical forests by means of remote sensing has become both increasingly popular and feasible with the advent of new satellite sensors. Satellite sensors of various spatial and spectral resolutions have been developed to take advantage of key spectral regions for vegetation: the visible (0.4-0.7um), the near infrared (NIR) (0.7-1.35um) and the mid-infrared (1.35-2.7um). However, since it's commercial availability, this technology has been used in several studies in all ecosystems with varying degrees of success (Gamon et al. 1995, Foody et al. 1996, Bohlman et al. 1998, Franklin et al. 2000, Lucas et al. 2000, Castro et al.

2002, Cihlar 2002, Tuomisto et al. 2003, among others). Both an understanding of the physical principles of passive remote sensing and image interpretation as well as consideration for the limitations of the technology are required if legitimate and insightful questions are to be explored.

From a passive remote sensing perspective, problems associated with monitoring LUCC illustrate the importance of understanding physiological processes in vegetation (ex. leaf senescence) and how those changes influence the interactions between vegetation and light. Leaf growth and leaf senescence are two are physiological processes that play a key role in our ability to extract information from satellite images (Walter-Shea and Norman 1991) acquired over areas with deciduous vegetation such as the *T-df*.

The main objectives of this thesis are 1) to explore the implications of the seasonality of foliage cover in the *T-df* for satellite remote sensing studies and 2) to explore the relationship between remotely sensed indices and foliage cover.

The main objective of Chapter 2 "Tropical Dry Climates" is to document aspects of leaf phenology in the tropical dry forest ecosystem (*T-df*) and their implications for satellite remote sensing. Emphasis is placed on presenting a description of the causes of leaf phenological change in this threatened ecosystem and their importance for conservation biology and land use/land cover change at the regional level.

The main objectives of Chapter 3 "Leaf area index measurements in a tropical moist forest: a case study from Costa Rica" are to 1) document the variability of leaf area index (LAI) in different stages of secondary growth in a

tropical moist forest, 2) explore functions that describe both the relationship and sensitivity of various spectral vegetation indices (SVIs) to a range of LAI values, 3) evaluate the difference between a classical least squares regression model and a more robust nonparametric regression model for linking LAI to SVIs and 4) compare the performance of SVIs in temperate regions from previous studies to the performance of the same indices in a tropical environment.

The main objectives of Chapter 4 "Species composition, similarity, diversity and leaf area index of three successional stages in a Costa Rican tropical dry forest" are to 1) describe the floristic composition, species diversity and similarity between three stages of secondary *T-df* regeneration through the use of ecological indices, 2) investigate the influence of the previous land use history on the species composition and 3) describe the changes in LAI as a function of the season and the successional stage.

A research question in progress that has been raised through the course of the previous chapters is addressed in Appendix A: The applicability of the optical LAI estimates from Santa Rosa to other *T-df* environments. This question is addressed as a comparison between the *T-df* in Palo Verde and Santa Rosa National Parks.

**1.2 References:**

Arroyo-Mora, J.P. 2002. Forest cover assessment, fragmentation analysis and

secondary forest detection for the Chorotega Region, Costa Rica. Master of Science Thesis. University of Alberta, Edmonton.

Bohlman S., Adams J.B., Smith M.O., and Peterson D.L. 1998. Seasonal foliage changes in the Eastern Amazon Basin detected from Landsat Thematic Mapper Satellite Images. Biotropica **30**:376-391.

Castro K.L., Sanchez-Azofeifa G.A., and Rivard B. 2003. Monitoring secondary tropical forests using space-borne data: implications for Central America. International Journal of Remote Sensing. **24**:1853-1874.

Cihlar J. 2002. Land cover mapping of large areas from satellites: status and research priorities. International Journal of Remote Sensing **21**:1093-1114.

Ewel J.J. 1999. Natural systems as models for the design of sustainable systems of land use. Agroforestry Systems **45**:1-21.

Foody G.M., Palubinskas G., Lucas R.M., Curran P.J., and Honzak J. 1996. Identifying terrestrial carbon sinks: Classification of successional stages in regenerating tropical forest from Landsat TM data. Remote Sensing of Environment **55**:205-216.

Franklin S.E., Dickson E.E., Farr D.R., Hansen M.J., and Moskal L.M. 2000. Quantification of landscape change from satellite remote sensing. The Forestry Chronicle **76**:877-886.

Gamon J.A., Field C.B., Goulden M.L., Griffin K.L., Hartley A.E., Joel G., Penuelas J. and Valentini R. 1995. Relationships between NDVI, canopy structure, and photosynthesis in three Californian vegetation types. Ecological Applications **5**:28-41.

Holdridge L. 1967. Life Zone Ecology. Tropical Science Center, San Jose, Costa Rica.

Leemans R. 1992. Global Holdridge Life Zone Classifications. Digital Raster Data on a 0.5-degree Cartesian Orthonormal Geodetic (lat/long) 360x720 grid. *in* Global Ecosystems Database Version 2.0. NOAA National Geophysical Data Center., Boulder, CO.

Lucas R.M., Honzak J., Curran P.J., Foody G.M., Milnes R., Brown T., and Amral S. 2000. Mapping the regional extent of tropical forest regeneration stages in the Brazilian Legal Amazon using NOAA-AVHRR data. International Journal of Remote Sensing **21**:2855-2881.

Murphy P.G., and Lugo A.E. 1986 Ecology of Tropical Dry Forest. Annual Review of Ecology and Systematics**17**:67-88.

Pfaff A.S.P., Kerr S., Hughes F., Liu S., Sanchez-Azofeifa G.A., Schimel D., Tosi J., and Watson V. 2000. The Kyoto protocol and payments for tropical forests: An interdisciplinary method for estimating carbon-offset supply and increasing the feasibility of a carbon market under the CDM. Ecological Economics **35**:203-221.

Piperno D.R., and Pearsall D.M. 2000. Origins of Agriculture in the Neotropics. Academic Press.

Sanchez-Azofeifa G.A. 1996. Assessing Land Use/Cover Change in Costa Rica. Doctoral Thesis. University of New Hampshire.

Sanchez-Azofeifa G.A., Calvo-Alvarado J.C., and Arroyo-Mora P. 2002. Dynamics of forest cover change in Costa Rica using Landsat Images

1986/87, 1996/97, 1997/2000. Pages 103 *in* Tropical Forests: Past, Present, Future. Smithsonian Tropical Research Institute, Panama City, Republic of Panama.

Tuomisto H., Poulsen A.D., Ruokolainen K., Moran R.C., Quintana C., Celi J., and Canas G. 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. Ecological Applications **13**:352-371.

Walter-Shea E.A., and Norman J.M. 1991. Leaf Optical Properties. Pages 229-252 *in* Myneni R.B. and Ross J., editors. Photon-Vegetation Interactions. Springer-Verlag, Berlin.

Figure 1.1: The American Tropics, bordered by the Tropics of Cancer and Capricorn.

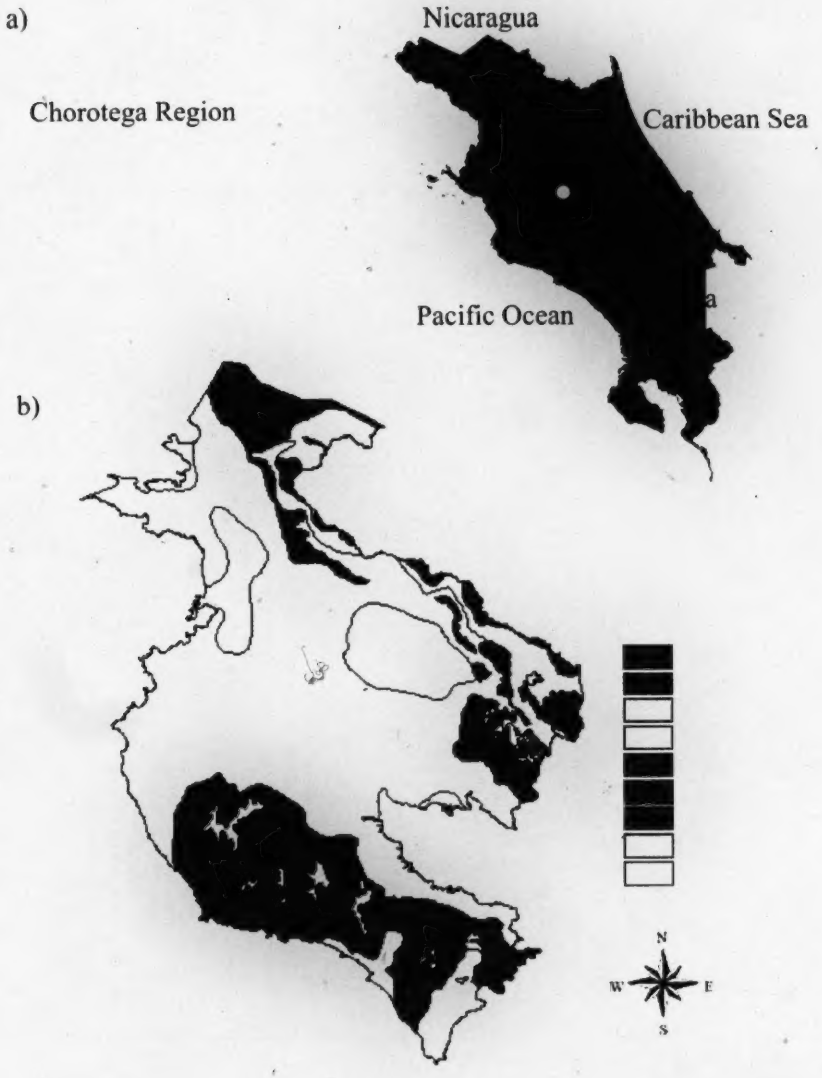



Figure 1.2. a) Chorotega Region in Costa Rica. b) Life Zones supported by the Chorotega Region. Transitional zones include areas with affinities of more than one life zone.

Figure 1. 3. Areas around the world with a favourable climate for supporting dry forest (dark gray) and moist forest (black) ecosystems. Spatial resolution: 0.5 degrees latitude by 0.5 degrees longitude (Leemans, 1992)

## 2.1 Introduction

Based on the Holdridge life zone system (Holdridge 1967) approximately 111,599,269 $km^2$ around the world have a climate favourable for dry forest (Leemans 1992, Figure 2.1). Of that area, 94% is located in the tropics. Tropical dry forests are found between the two parallels of latitude, the Tropics of Cancer and Capricorn (23°27' N and S) where there are several months of little or no precipitation (Holdridge 1967). In general, three to seven month's dry season duration has been quoted for seasonally dry forests (Janzen 1983; Murphy and Lugo 1986; Luttge 1997; Piperno and Pearsall 2000). The tropical dry forest ecosystem is one of the most fragile and least protected ecosystems in the world.

In general, Neotropical dry forests are less species rich than moist or wet forests. For example, 430 species of woody plants have been recorded in the wet forest of La Selva Biological Station, Costa Rica (Hartshorn and Hammel 1994), while in the dry forest of the Santa Rosa National Park, Costa Rica, 160 species (51 families) have been inventoried (Kalácska and Sánchez-Azofeifa, unpublished data). In addition, Gentry (1995) reports a range of 21–121 species (9 and 41 families) from various 0.1ha plots around the Neotropics. However, there is more structural (e.g., wood specific gravity) and physiological (e.g., growth seasonality) diversity in the plant life forms of dry forests than in wet forests (Medina 1995).

Tropical forests that once formed a continuous habitat across Mesoamerica and some regions of the Pacific and Atlantic regions of South-

---

This chapter has been published as: Sanchez-Azofeifa G.A., Kalacska M., Quesada M., Stoner K.E., Lobo J.A., and Arroyo-Mora. P. 2003. Tropical Dry Climates. *in* Schwartz M.D., editor. Phenology: An Integrative Environmental Science. Kluwer Academic Press. In Press.

America, are now found in fragmented patches (Whitmore and Sayer 1992; Heywood et al. 1994; Trejo and Dirzo 2000). Tropical deforestation is likely to affect both biotic and abiotic factors that control the phenological expression of plant communities with severe consequences to plant populations and the communities that interact or depend on them (Cascante et al. 2002; Fuchs et al. 2003, in press). However, fortunately in certain regions of the Neotropics such as in Costa Rica, the secondary forests are in a state of regeneration through which the dry forests are also starting to recuperate (Arroyo-Mora 2002).

Both savannahs and dry forests (T-df) can co-occur in areas with the same climate, but the dry deciduous forests have a tendency to be found in areas with greater soil fertility (Ratter et al. 1973; Mooney et al. 1995). In many areas however, the occurrence of either savannah or dry forest is principally controlled by human disturbance (Maass 1995; Menaut et al. 1995).

Due to the favorable climatic conditions in which they are found, tropical dry forests have been heavily exploited for agriculture (Ewel 1999). Piperno and Pearsall (2000) argue that historically, tropical wet and dry forests had completely different associations with human activities. They state that the deciduous and semi-evergreen forests (especially the T-df) were the locations of the majority of the early human settlements in addition to being the home of the wild ancestors of many crop plants as well as the origin of animal husbandry. Even today, in most tropical countries, the majority of the agriculture and pasturelands are located in areas that used to be dry and moist forest. This pattern of both higher population density as well as higher intensity food production in the T-df as compared to

wetter life zones may be a reflection of the historical tendency for humans to settle these areas (Piperno and Pearsall 2000). It appears that the tuberous plants that are rich in starch for human consumption seem to be more common in the seasonal forests, since the tuber is developed in part for energy storage during the dry season. The long dry season aided in burning of the vegetative cover in order to prepare the fields for agriculture (Piperno and Pearsall 2000). In addition, weeds and pests are less aggressive in the drier environments (Murphy and Lugo 1986).

Tropical dry forest phenology is an area that is still in its early stages of academic discovery, since historically more emphasis has been placed on tropical evergreen forests, especially the Amazon Basin (Luttge 1997). Therefore, there is a need for continuous and systematic efforts to understand its phenological patterns and integrate its phenological mechanisms at two basic levels: 1) In the context of conservation biology and 2) the context of land use and land cover change that are taking place on this rich agricultural frontier. In this chapter we document different aspects related to leaf phenology in the tropical dry forest ecosystem and its implications for satellite remote sensing. Emphasis is placed on presenting a description of the causes of leaf phenological change in this threatened ecosystem, and how these can be linked with conservation biology and land use/land cover change at the regional level.

## 2.2 Causes of Phenological Change

Several studies have indicated that the phenological expression of leaves, flowers and fruits are affected by biotic and abiotic factors. Abiotic factors such as changes in water level stored by plants (Reich and Borchert 1984; Borchert 1994, but also see Wright and Cornejo 1990; Wright 1991), seasonal variations in rainfall (Opler et al. 1976), changes in temperature (Ashton et al. 1988; Williams-Linera 1997) photoperiod (Leopold 1951; Tallak et al. 1981; van Schaik 1986), irradiance (Wright and van Schaik 1994) or sporadic climatic events (Sakai et al.1999), have been proposed as the main causes of leaf production or leaf abscission in tropical dry forest plants. In contrast, biotic factors, such as competition for pollinators or pollinator attraction (Robertson 1895; Janzen 1967; Gentry 1974; Stiles 1975; Appanah 1985; Murray et al. 1987; Sakai et al. 1999; Lobo et al. in press), competition for seed dispersers, and avoidance of herbivory (Marquis 1988; Aide 1993; van Schaik et al. 1993) have been considered as the factors regulating the intensity and duration of leaf and flower production. The abiotic and biotic factors are not mutually exclusive, and it is likely that several are interacting to regulate the expression of each phenological phase.

In tropical dry forests, apart from foliage seasonality, relationships between water availability and the structural and physiological characteristics such as hydraulic architecture or sensitivity to water stress produce a variety of phenological behaviors (Murphy and Lugo 1986; Bullock 1995; Holbrook et al. 1995; Luttge 1997, among others). However, due to the remote sensing component of this chapter, the discussion in this section will be largely limited to

phenological changes in leaf cover, even though most studies that evaluate the effect of abiotic and biotic factors on the phenological expression of tropical plants (both dry and wet forests) have mainly studied leaf, but not flower or fruit phenology.

One of the major causes of the leaf phenological patterns (as mentioned above) in all tropical dry forest is the length of the dry season. This difference may be partly responsible for the differences in physical characteristics such as canopy height or biomass. Apart from leaf phenology, the length of the dry season and the seasonality of precipitation are also important for evolutionary adaptations of gene and seed dispersal, which are distinct in dry forests from the wet forests. In general, in dry forests most trees have conspicuous flowers and wind-dispersed seeds. Dry forests also have a lower biomass and a smaller stature than wet forests (Gentry 1995). Two other main factors that influence leaf phenological patterns are edaphic associations and topography since they determine the spatial heterogeneity of the available water (Murphy and Lugo 1995).

Water stress can vary at both regional and local scales. This variability induces a multitude of tree life forms with different leaf phenological patterns (Mooney et al. 1995). At the regional scale, the structure of the forest is greatly affected. It has been shown that as water availability decreases, so does the number of canopy stories as well as the horizontal continuity of the canopy (Murphy and Lugo 1995). Figure 2.2 compares the climate diagrams (Walter 1971) for fourteen sites from different life zones, ranging from wet to dry forests in Costa Rica as well as the dry forest in Chamela, Mexico. The mean monthly

temperature (°C) and the monthly precipitation (mm) are scaled to represent the potential evapotranspiration. Dry months are represented by dotted areas, humid months by the vertical lines, and months with rain in excess of 100mm are in solid black. Differences in the severity of the dry season as well as the pattern of the rainfall can cause the different leaf phenological patterns observed at various sites. For example, in Guanacaste, Costa Rica, Gentry (1995) estimates that 40-60% of the tree species are deciduous whereas over 70% are deciduous in Chamela, Mexico, where the severity of the dry season is more pronounced (Figure 2.2).

The general leaf phenological response to the dry season is drought deciduousness where the woody plants lose their leaves in the dry season, but there are exceptions (wet season deciduous, Fanjul and Barradas 1987) as well as dry evergreen forests and evergreen succulent plants in dry forests (Gentry 1995; Holbrook et al. 1995). Occasional anomalous rains in the dry season and drought spells in the wet season complicate this variation in resource availability in the rainy season. The growing periods are thus affected by the variability in flushing as it occurs in response to anomalous rains in the dry season or variation in the drying out process (Murphy and Lugo 1995). In a comparison between wet (La Selva) and dry (Comelco) sites in Costa Rica, Frankie et al. (1974) found that the forest at La Selva maintained its evergreen appearance throughout the year. However, even this wet forest experienced increased leaf flushing with the onset of the wet season. In Comelco they found that while leaf fall began as early as October, the majority of the trees lost their leaves in the dry season, with the peak

in leaf fall occurring in March. Of the 113 species they inventoried at Comelco, 83 partially or completely lost their leaves and 19 were evergreen (ex. *Clusia rosea, Staryx argenteus*). The trees in the Riparian zones lost their leaves, but were simultaneously replaced. One species, *Lysiloma seemannii* had an unusual leaf-flushing pattern in that after it lost its leaves in the dry season, the new leaves did not appear until one month after the rainy season began. Certain species also brought new leaves in January and March but most of these species (for example, *Anacardium excelsum, Coccoloba padiformis*) were from the Riparian zones. In total, Frankie et al. (1974) found that 75% of the species are affected by the seasonality of the precipitation in the dry forest, compared to 17% in the wet forest. The timing of leaf flushing was also found to be very different: in the wet forest, most of the leaves were produced in the dry season, whereas in the dry forest the leaves were produced at the beginning of the wet season.

**2.3 Conservation Biology**

In this section, we review the literature and present some of the main consequences that change or disruption of plant phenology may have on the viability of plant populations and animal communities that interact with them.

Biotic factors, such as competition for pollinators or pollinator attraction have been interpreted as important adaptive forces responsible for phenological patterns in tropical plants (Robertson 1895; Janzen 1967; Gentry 1974; Stiles 1975; Appanah 1985; Murray et al. 1987; Zimmerman et al. 1989; Sakai et al. 1999; Lobo et al., in press). A disruption of the flowering phenological patterns

caused by disturbance or fragmentation is likely to affect the behavior and visitation rate of pollinators. Fragmented landscapes reduce the amount of resources available, as well as appropriate areas for roosting and perching for nectarivorous bats and birds that serve as important pollinators for many tropical plant species (Feinsinger et al. 1982; Andren and Angelstran 1988; Bierregaard and Lovejoy 1989; Rolstad 1991; Saunders et al. 1991; Helverson 1993; Quesada et al., in press). If the flowering pattern of plants that share pollinators of the same guild is displaced over time (Frankie et al. 1974; Stiles 1975; Fleming 1988), competition for the same pollinators will occur, resulting in negative consequences for the reproductive success of the plants and the ability of the pollinators to obtain resources over time. For example, in the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve, Mexico, trees of the family Bombacaceae provided the main resource to the nectarivorous bats *Leptonycteris curasoae* during 8 months and *Glossophaga soricina* during 6 months. Both bat species concentrated on one bombacaceous species each month (Stoner et al. 2003). The sequential use of bombacaceuos species by these bats coincided with the flowering phenology of the tree species. These data suggest that changes in the flower phenology caused by habitat disruption may result in competition between these bat species and ultimately may result in local extinction, especially of endemic species that are common in this dry forest. A rare endemic nectarivorous bat that is only found in 4 states in Mexico, *Musonycteris harrisoni*, foraged on the bombacaceous tree *Ceiba grandiflora* during 3 months of the year (Stoner et al. 2002). Since this species has such a restricted distribution and is a

specialist nectarivore, changes in flower phenology could be catastrophic for populations of this bat.

Timing of leaf flushing directly affects insect herbivores that depend upon flushing species to complete part of their life cycle (Janzen 1970, 1983; Dirzo and Dominguez 1995). Phenological changes caused by habitat loss will also disrupt the pollination patterns of many long-distance pollinators and trap-liners such as some large bees, hawkmoths, nectarivorous bats, and hummingbirds that have been shown to follow the flowering phenology of plants (Stiles 1977; Haber and Frankie 1989; Frankie et al. 1998; Fleming et al. 1993; Haber and Stevenson 2003). For example, in Costa Rica, hawkmoths regularly move from the lowland tropical dry forest to surrounding areas at higher elevations, following patterns of flowering resources (Haber and Stevenson 2002). Similarly, in México and the southwestern U.S. some nectarivorous bats have been shown to migrate following the availability of flower resources, mainly from the family Cactaceae and Agavaceae (Fleming et al. 1993).

Intra-specific variation in the frequency, duration, amplitude and synchrony of flowering by individuals also has been proposed as an important factor that affects the reproduction and the genetic structure of tropical plant populations in disturbed habitats (Murawski et al. 1990; Murawski and Hamrick 1992; Newstrom et al. 1994; Doligez and Joly 1997; Nason and Hamrick 1997). Flowering phenology directly determines the effective number of pollen donors and the density of flowering individuals, both of which affect the patterns of pollen flow between trees (Stephenson 1982; Murawski and Hamrick 1992).

Plants with asynchronous flowering may experience a decrease in reproductive output, the amount of pollen, the number of pollen donors and the levels of outcrossing compared to individuals blooming during the same period. Fuchs et al. (2003) suggested that pollinator behavior is likely to change the mating patterns of *P. quinata*. This study showed that in disturbed fragmented habitats or in trees with early or late peak flowering, bat pollinators are more likely to promote selfing within trees (i.e., geitonogamy) and they have a tendency to produce singly sired fruits, whereas in undisturbed natural forests outcrossing is higher and multiple paternity is more common. The long-tongued bat (*Glossophaga soricina)*, one of the main pollinators of *P. quinata*, has been shown to adopt a territorial behavior within a single plant in disturbed isolated environments with limited resources (Lemke 1984, 1985).

The timing of fruiting during the year, which may be altered as a result of environmental changes associated with habitat disturbance, may affect potential vertebrate seed dispersers that, in turn, may affect the reproductive success of the plants they disperse (Flemming and Sosa 1994). Frugivorous Old World and New World bats are known to migrate or change habitats depending on the availability of fruit resources (Eby 1991; Stoner 2001). Similarly, the abundance of temperate and altitudinal migrant birds in tropical forests is closely associated with fruit abundance (Levey et al. 1994). Furthermore, displacement of fruiting phenology of tree species that are keystone resources because they provide fruits when resources are relatively scarce, could have negative consequences on populations of birds and mammals that disperse their seeds and ultimately

negative effects on recruitment of the species they disperse (Howe 1984). Seed dispersal by animals is negatively affected by deforestation and results in lower recruitment in forest fragments.

Another factor affected by forest fragmentation is seed predation. In a tropical dry forest seed predation by bruchid beetles on the tree *Samanea saman* was higher in populations of trees found in continuous forest and found to be much less in isolated trees. The bruchid beetles, *Merobruchus columbinus* and *Stator limbatus* (Bruchidae) are specific seed predators of *S. saman* (Janzen 1978). It is likely that the populations of these bruchid species are affected by density dependent factors related to the availability and fluctuation of food resources within fragments, including seeds and flowers. Another explanation is that adult bruchids have to fly greater distances to find isolated trees than trees in continuous populations. This pattern of higher seed predation in populations from continuous forest also has been observed in the dry forest tree, *Bahuinia pauletia.* Finally, the ultimate consequences of habitat reduction and phenological disruption is a decrease in reproductive plants, increasing the negative effects of endogamy, reducing the quantity and quality of pollen, and lowering the genetic variability of the progeny (Cascante et al. 2002). This likely will affect the viability and establishment of plant populations over time.

**2.4 Phenology and Land Use / Cover Change**

Remote sensing data provides the possibility for an instantaneous look at a large area with the opportunity of acquiring frequent repeat imagery for the same

area. This is important for phenological studies because the temporal variability of the ecosystem can be captured at large scales. In particular, it is essential to consider leaf phenology in order to correctly characterize areas of deciduous forest. Since they measure surface reflectance, optical sensors have been widely used for land cover classification and characterization. However, it must be taken into consideration that one of the greatest limitations to optical sensors is cloud cover. And in the tropics, cloud cover is especially prevalent in the wet season. Cloud free imagery is more easily acquired during the dry season, where in deciduous forests, the majority of the trees are leafless (Arroyo-Mora J.P. 2002). In addition, vegetation studies using reflectance data have generally focused on green leaves, with both dry vegetation and non-green components being neglected in comparison (van der Meer 1999). However, in areas of deciduous forest green leaves will not always dominate the spectral signature of the forest. In the dry season, only a small fraction of the spectra will be representative of green foliage. The majority of the pixels will be representing leaf litter, bark, branches and soil in various combinations. Therefore, this temporal variability of the spectral signatures that can be extracted from imagery must be taken into consideration in such environments.

As an example, two false color composite images of the same area of dry forest surrounding the Chamela Biological Station, Mexico, were acquired during the dry (March) and wet (August) seasons from the Landsat 7 ETM+ sensor (not shown). While the two images visually look completely different, more importantly, the spectral signature of the forest also changes with the seasons.

This is key because many algorithms rely on spectral signatures to classify areas. If the same unsupervised classification algorithm (Isodata) is run on the two images, 180 $km^2$ of forest cover is extracted from the wet season image, while only 26 $km^2$ of land cover exhibits the spectral signature of forest in the dry season (Kalacska et al. 2001). In the dry season image, only the Riparian areas appear to have forest cover.

In a similar case study from the Santa Rosa National Park, Costa Rica, two images (dry season – April and wet season – October) of Landsat TM 5 were classified using an unsupervised classification into forest and non-forest classes. From the wet season image, 61$km^2$ of forest were extracted, whereas from the dry season image only 18 $km^2$ were classified as forest (Kalacska et al. 2001). The discrepancy in the amount of forest extracted from the images in the two seasons is because dry deciduous forests where trees loose their leaves, may seem to have the spectral signature of pasturelands or agricultural fields in the dry season (Figure 2.3).

In the wet season, (Figure 2.3a) the spectra for both the evergreen and deciduous components of the forest are similar. However, in the dry season (Figure 2.3b), the spectral signature of the deciduous forest no longer resembles that of the evergreen forest. In fact, there is more than a 20% difference in the near infrared band (band 4) between the two forest classes in the dry season. While these results are important at a local scale, their implications become more profound if regional or global scales are considered. For example, Sader and Joyce (1988) reported the total forest cover for Costa Rica as 17%. If their map

of forest distribution is examined, it can be seen that the province of Guanacaste and the Nicoya Peninsula, both with large extents of deciduous forest, are shown as almost completely non-forest. In a more recent classification of Guanacaste and the Nicoya Peninsula, using Landsat 7 ETM+ imagery, Arroyo-Mora (2002) shows that the forest cover is actually 45%. At the national scale, in the most recent remotely sensed forest cover inventory to date of the entire country of Costa Rica, Sanchez-Azofeifa et al. (2002) report a total forest extent 58% greater than the other previous studies (Castro-Salazar and Arias-Murillo 1998). Seasonal changes in leaf phenology in the deciduous forest are part of the reason for those differences. Even at the spatial resolution of most global monitoring systems (1km) significant areas of forest can be missed if only dry season images are used or if the phenological changes in leaf cover are not taken into consideration. This forest, which has been ignored by previous remote sensing analysis, is not uniform and includes different stages of succession with different levels of deciduousness (Arroyo-Mora 2002). For example, in the recent global land cover classification from the MODIS Land Cover Classification Program, neither the area encompassing the Chamela Biological Station, Mexico nor the Santa Rosa National Park, Costa Rica is classified as forest. These complications are important not only for classification purposes, but also in many cases outputs from such data sets are used in global models like CENTURY. The calculations from such models are then further used to calculate baselines and benefits of a given policy for carbon sequestration, for example.

## 2.5 Final Remarks

Since so many organisms depend upon phenological patterns in tropical forests, it is crucial to document how these phenological patterns may be changed by deforestation and the resulting habitat fragmentation. Future studies on phenological patterns of tropical plants should attempt to document intra-specific variation within distinct habitat types and under different levels of disturbance, in order to provide a clear understanding of ecosystem phenological response to different levels and types of disturbance. This information will be important in quantifying the effects of forest fragmentation on phenological patterns and ultimately on tropical ecosystems.

A wealth of information is available on studies conducted with remotely sensed data in both the temperate and tropical regions. And while the image processing techniques may be similar, the ground validation techniques are very different in certain aspects. The complexity (structural and temporal) of the tropical deciduous forests also requires special consideration when field data are being collected. In certain cases, for example when collecting Leaf Area Index (LAI), new sampling techniques need to be developed to account for the spatial and temporal heterogeneity of the forest. This is also the case if there are certain specific phenological patterns of interest. Both the scale of the sampling, as well as the technique should be determined by the required data. For example, biophysical parameters of the canopy such as LAI, vegetation fraction (VF) and the fraction of photosynthetically active radiation ($f_{PAR}$) have been successfully linked to remotely sensed data in many studies in conifer stands, temperate broad

leaf forests and agricultural fields (Chen and Black 1991; Price and Bausch 1995; Chen and Cihlar 1996; Chen et al. 1997). However, similar techniques have not been as thoroughly explored in tropical dry forest environments, nor is there a clear understanding of the impact of phenology in these important biophysical variables. In addition, with the exception of a few studies such as Arroyo-Mora (2002) or Clark (2002) optical remote sensing studies in tropical environments have been predominantly conducted with either the Landsat (TM and ETM+) or AVHRR sensors. However, high spatial resolution multispectral sensors such as IKONOS (4 and 1m spatial resolution and 4 spectral bands) and Quickbird (2m and 60cm spatial resolution, 4 spectral bands) have begun acquiring substantial worldwide archives and can play a key role in monitoring phenological processes in tropical dry forest environments. Also, with the introduction of ASTER (15m spatial resolution, 14 spectral bands) data can be obtained quite economically. All three of these sensors may be used to capture detailed temporal changes in the dry deciduous forest. In addition, ALI (Advanced Land Imager) a new sensor from the EO-1 platform provides a more cost effective alternative for acquiring Landsat-type data.

Increased spectral resolution may also be an option to characterize deciduous forests from a remote sensing point of view. Hyperspectral sensors such as Hyperion (30m spatial resolution and 220 spectral bands) or the air-borne sensor HYDICE (1m spatial resolution and 220 bands) offer new possibilities for describing the phenological changes in the deciduous forest, but their application will be limited to the short life span of this sensor type. More small changes at

the canopy level can be observed with these sensors than can be captured by multispectral sensors. These changes can be correlated to ground measurements such as chlorophyll concentrations as a function of age and complexity in order to begin modeling the seasonal changes in the ecosystem in greater detail. Hyperspectral data sets will provide a greater range of possibilities for deriving indices that may be more sensitive to the vegetation characteristics, as well as to phenological changes in dynamic environments.

**2.6 References**


Aide, T. M., Patterns of leaf development and herbivory in a tropical understory community, *Ecology, 74*, 455-466, 1993.

Andren, H., and P. Angelstarn, Elevated predation rates as an edge effect in habitat islands, *Ecology*, *69*, 544-547, 1988.

Appanah, S., General flowering in the climax rain forest of Southeast Asia, *Journal of Tropical Ecology, 1*, 225–240, 1985.

Arroyo-Mora, P., *Forest cover assessment, Chorotega Region, Costa Rica*, Unpublished M.Sc. Thesis, Department of Earth and Atmospheric Sciences, University of Alberta, Canada, 2002.

Ashton, P. S., T. J. Givnish, and S. Appanah, Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics, *The American Naturalist*, *231*, 44–66, 1988.

Bierregaard, R. O., and T. E. Lovejoy, Effects of forest fragmentation on Amazonian understory bird communities, *Acta Amazonica 19*, 215-241, 1989.

Borchert, R., Soil and stem water storage determine phenology and distribution of tropical dry forest trees, *Ecology, 75,* 1437–1449, 1994.

Bullock, S. H., Plant reproduction in Neotropical dry forests, in *Seasonally Tropical Forests*, edited by H. A. Mooney, S. H. Bullock, and E. Medina, pp. 277-303, Cambridge University Press, Cambridge, UK, 1995.

Cascante, A., M. Quesada, J. A. Lobo, and E. J. Fuchs, Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree, *Samanea saman*, *Conserv. Biol., 16,* 137-147, 2002.

Castro-Salazar, R., and G. Arias-Murillo, Costa Rica: Toward the sustainability of its forest resources, *Technical Report Fonda Nacional de Financiamiento Foresta (FONAFIFO)*, San Jose, Costa Rica, 1998.

Chen, J. M., and T. A. Black, Measuring leaf area index of plant canopies with branch architecture, *Agricult. Forest Met., 57,* 1-12, 1991.

Chen, J. M., and J. Chilar, Retrieving leaf area index of boreal forests using Landsat TM images, *Remote Sens. Environ., 55,* 153-162, 1996.

Chen, J. M., P. M. Rich, S. T. Gower, J. M. Norman, and S. Plummer, Leaf area index of boreal forests: Theory, techniques and measurements, *J. Geophys. Res. 102*, 429-443, 1997.

Clark, D., Applications of 1m and 4m resolution satellite imagery to studies of tropical forest ecology, management and secondary forest detection, in

*Tropical Forests: Past, Present, Future*, p. 20, The Association of Tropical Biology Annual Meeting, Smithsonian Tropical Research Institute, 2002. pp 20

Dirzo, R., and C. A. Dominguez, Plant-herbivore interactions in Mesoamerican tropical dry forests, in *Seasonally dry tropical forests*, edited by S. H. Bullock, H. A. Mooney, and E. Medina, pp. 277-303, Cambridge University Press, Cambridge, 1995.

Doligez A., and H. Joly, Genetic diversity and spatial structure within a natural stand of a tropical forest tree species, *Carapa procera* (Meliaceae), in French Guiana, *Heredity, 79*,72-82, 1997.

Eby, P., Seasonal movements of grey-headed flying-foxes, *Pteropus poliocephalus* (Chirpotera: Pteropodidae), from two maternity camps in northern New South Wales, *Wildlife Research, 18,* 547-559, 1991.

Ewel, J., Natural systems as models for the design of sustainable systems of land use, *Agroforestry Systems, 45*, 1-21, 1999.

Fanjul, L. and V.L. Barradas, Dirunal and seasonal variation in the water relations of some deciduous and evergreen trees of a deciduous dry forest of the western coast of Mexico, *J. Appl. Ecol., 24*, 289-303, 1987.

Feinsinger, P., J. A. Wolfe, and L. A. Swarm, Island ecology: reduced hummingbird diversity and the pollination biology of plants on Trinidad and Tobago, West Indies, *Ecology, 63*, 494-506, 1982.

Fleming, T. H., *The short-tailed fruit bat: A study in plant-animal interactions*, University of Chicago Press, Chicago, 365 pp., 1988.

Fleming, T. H., R. A. Nuñez, and L. S. L. Sternberg, Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis, *Oecologia, 94,* 72-75, 1993.

Flemming, T. H. and V. J. Sosa, Effects of nectarivorous and frugiviorous mammals on reproductive success of plants, *J. Mammalogy, 75,* 845-851, 1994.

Frankie, G. W., H. G. Baker, and P. A. Opler, Comparative phenological studies of tress in a tropical lowland wet and dry forest sites of Costa Rica, *J. Ecology, 62,* 881-913, 1974.

Frankie, G. W., S. B. Vinson, M. A. Rizzardi, T. L. Griswold, Diversity and abundance of bees visiting a mass flowering tree species in disturbed seasonal dry forest, Costa Rica, *Journal of the Kansas Entomological Society, 70,* 281-296, 1998.

Fuchs, E. J, J. A. Lobo and M. Quesada. Effects of forest fragmentation and flowering phenology on the reproductive success and mating patterns on the tropical dry forest tree, *Pachira quinata* (Bombacaceae), *Conservation Biology* 17:17:149-157. 2003

Gentry, A. H., Flowering phenology and diversity in tropical Bignoniaceae, *Biotropica, 6,* 64- 68, 1974.

Gentry, A. H., Diversity of floristic composition of Neotropical dry forests, in *Seasonally Tropical Forests*, edited by H. A. Mooney, S. H. Bullock, and E. Medina, pp. 146-194, Cambridge University Press, Cambridge, UK, 1995.

Haber, W. A. and G. W. Frankie, A tropical hawkmoth community: Costa Rican dry forest Sphingidae, *Biotropica, 21*, 155-172, 1989.

Haber, W. A., and R. Stevenson, Diversity, migration, and conservation of butterflies in northern Costa Rica, in *Biodiversity Conservation in Costa Rica: Learning the Lessons in a Seasonal Dry Forest*, edited by G.W. Frankie, A. Mata, and S.B. Vinson, University of California Press, Berkeley, California, 2002.

Hartshorn, G., and B. E. Hammel, Vegetation types and floristic patterns, in *La Selva, Ecology and Natural History of a Neotropical Rain Forest*, edited by L. McDade, K. S. Bawa, H. A. Hespenheide, and G. Hartshorn, pp. 73-89, University of Chicago Press, Chicago, 1994.

Helversen, O. V., Adaptations of flowers to the pollination by Glossophaginae bats, *Animal-plant interactions in tropical environments,* edited by W. Barthlott, pp. 41-49, Alexander Koenig Museum, Bonn, Germany, 1993.

Heywood, V. H., G. M. Mace, R. M. May, and S. N. Stuart, Uncertainties in extinction rates, *Nature, 368*, 105, 1994.

Holbrook, N. M., J. L. Witbeck, and H. A. Mooney, Drought responses of Neotropical dry forest trees, in *Seasonally Tropical Forests*, edited by H. A. Mooney, S. H. Bullock, and E. Medina, pp. 243-276, Cambridge University Press, Cambridge, UK, 1995.

Holdridge L., *Life Zone Ecology*, Tropical Science Centre, San Jose, Costa Rica, 206 pp., 1967.

Howe, H. F., Implications of seed dispersal by animals for tropical reserve management, *Biological Conservation*, *30*, 261-281, 1984.

Janzen, D. H., Synchronization of sexual reproduction of trees within dry season in Central America, *Ecology, 21*, 620–637, 1967.

Janzen, D. H., Herbivores and the number of tree species in tropical forests, *American Naturalist, 104*, 501-528, 1970.

Janzen, D. H. 1978. Reduction of seed predation on Bauhinia pauletia (Leguminosae) through habitat destruction in a Costa Rican deciduous frest. Brenesia 14/15:325-336

Janzen, D. H., *Costa Rica Natural History*, University of Chicago Press, Chicago, 816 pp., 1983.

Kalácska, M., G. A. Sánchez-Azofeifa, B. Rivard, P. Arroyo-Mora, R. Hall, J. Zhang, and K. Dutchak, Implications of phenological changes in the extraction of Mesoamerican Tropical Dry Forests through remote sensing: A case study from Costa Rica and Mexico, Proceedings of the International Conference, pp. 84-85, Wageningen University, The Netherlands, 2001.

Leemans, R., Global Holdridge Life Zone Classifications, Digital Raster Data, in *Global Ecosystems Database Version 2.0*, NOAA National Geophysical Data Center, Boulder, Colorado, 1992.

Lemke, T. O., Foraging ecology of the long-nosed bat *Glossophaga soricina* with respect to food availability, *Ecology, 65*, 538-548, 1984.

Lemke, T. O., Pollen carrying by the nectar-feeding bat *Glossophaga soricina* in a suburban environment, *Biotropica, 17*, 107-111, 1985.

Levey, D. J., T. C. Moermond, and J. S. Denslow, Frugivory: an overview, in *La Selva, Ecology and Natural History of a Neotropical Rain Forest*, edited by L. McDade, K. S. Bawa, H. A. Hespenheide, and G. Hartshorn, pp. 282-294, University of Chicago Press, Chicago, 1994.

Leopold, A. C., Photoperiodism in plants, *Quarterly Review of Biology*, *26*, 247-263, 1951.

Lobo, J. A., M. Quesada, K. E. Stoner, E. J. Fuchs, and Y. Herrerías-Diego, Latitudinal variation of phenological patterns of bombacaceous species in seasonal forests in Costa Rica and Mexico, *Amer. J. Botany*, (in press), 2003.

Luttge, U., *Physiological ecology of tropical plants*, Spriger-Verlag, Heidelberg, 384 pp., 1997.

Marquis, R. J., Phenological variation in the Neotroical understory shrub *Piper arieianum*: causes and consequences, *Ecology, 69*, 1552-1565, 1988.

Maass, J. M., Conversion of tropical dry forest to pasture and agriculture, in *Seasonally Tropical Forests*, edited by H. A. Mooney, S. H. Bullock, and E. Medina, pp. 399-422, Cambridge University Press, Cambridge, UK, 1995.

Medina, E., Diversity of life forms of higher plants in Neotropical dry forests, in *Seasonally Tropical Forests*, edited by H. A. Mooney, S. H. Bullock, and

E. Medina, pp. 221-242, Cambridge University Press, Cambridge, UK, 1995.

Menaut, J. C., M. Lepage, and L. Abbadie L., Savannas, woodlands and dry forests in Africa, in *Seasonally Tropical Forests*, edited by H. A. Mooney, S. H. Bullock, and E. Medina, pp. 64-92, Cambridge University Press, Cambridge, UK, 1995.

Mooney, H.A., S. H. Bullock, and E. Medina, *Seasonally Tropical Forests*, Cambridge University Press, Cambridge, UK, 450 pp., 1995.

Murphy, P.G. and A. E. Lugo, Ecology of tropical dry forest, *Annual Review of Ecology and Systematics*, *17*, 67-88, 1986.

Murphy, P.G., and A. E. Lugo, Dry forests of Central America and the Caribbean, in *Seasonally Tropical Forests*, edited by H. A. Mooney, S. H. Bullock, and E. Medina, pp. 9-34, Cambridge University Press, Cambridge, UK, 1995.

Murawski, D. A., J. L. Hamrick, S. P. Hubbell, and R. B. Foster, Mating systems of two bombacaceous trees of a Neotropical moist forest. *Oecologia, 82*, 501-506, 1990.

Murawski, D. A., and J. L. Hamrick, Mating system and phenology of *Ceiba pentandra* (Bombacaceae) in Central Panama, *J. Heredity, 83*, 401-404, 1992.

Murray, K. G., P. Feinsinger, W. H. Busby, Y. B. Linhart, J. H. Beach, P. Kinsman, Evaluation of character displacement among plants in two tropical pollination guilds, *Ecology, 68*, 1283–1293, 1987.

Nason, J. D., and J. L. Hamrick, Reproductive and genetic consequences of forest fragmentation: two case studies of neotropical canopy trees, *J. Heredity, 88,* 264-276, 1997.

Newstrom, L. E., G. W. Frankie, H. G. Baker, and R. K. Colwell, Diversity of long-term flowering patterns, in *La Selva, Ecology and Natural History of a Neotropical Rain Forest*, edited by L. McDade, K. S. Bawa, H. A. Hespenheide, and G. Hartshorn, pp. 142-160, University of Chicago Press, Chicago, 1994.

Opler, P. A., G. W. Frankie, and H. G. Baker, Rainfall as a factor in the release, timing, and sychronization of anthesis by tropical tress and shrubs, *J. Biogeography, 3,* 231-236, 1976.

Piperno, D. R., and D. M. Pearsall, *Origins of Agriculture in the Neotropics,* Academic Press, New York, 400 pp., 2000.

Price, J. C., and W. C. Bausch, Leaf area index estimation from visible and near-infrared reflectance data, *Remote Sens. of Environ., 52*, 55-65, 1995.

Quesada, M., K. E. Stoner, V. Rosas-Guerrero, C. Palacios-Guevara, and J. Lobo, Effects of habitat disruption on the activity of nectarivorous bats (Chiroptera: Phyllostomidae) in a dry tropical forest: implications for the reproductive success of the neotropical tree *Ceiba grandiflora, Oecologia*, 135: 400-406. 2003.

Ratter, J.A., P. W. Richards, G. Argent, and D. R. Gifford, Observations of the vegetation of northeastern Mato Frosso. I. The woody vegetation types of

the Xavantina-Cachimbo expedition area, *Philosophical Transactions of the Royal Society of London, Series B, 266*, 449-492, 1973.

Reich, P. B. and R. Borchert, Water stress and tree phenology in a tropical dry forest in the tropical dry forest lowlands of Costa Rica, *J. Ecology, 72,* 61-74, 1984.

Robertson, C., The philosophy of flower seasons, and the phenological relations of the entomophilous flora and the anthophilous insect fauna, *American Naturalist, 29*, 97-117, 1895.

Rolstad, J., Consequences of forest fragmentation for the dynamics of bird populations: Concelptual issues and the evidence, *Biological Journal of the Linnean Society, 42*, 149-163, 1991.

Sader, S., and A. T. Joyce, Deforestation rates and trends in Costa Rica, 1940 to 1983, *Biotropica, 20*(1), 11-19, 1988.

Sakai, S., K. Momose, T. Yumoto, T. Nagamitsu, H. Nagamasu, A. A. Hamid, and T. Nakasiiizuka, Plant reproductive phenology over four years including an episode of general flowering in a lowland Dipterocarp forest, Sarwak, Malaysia, *Amer. J. Botany, 86,* 1414–1436, 1999.

Sanchez-Azofeifa, G.A. and Calvo J., *Final report on the extent to Costa Rica forest cover: Year 2002*, Costa Rican National Forest Financing Fund, 20 pp., 2002.

Saunders, P. A., Jr., R. J. Hobbs and C. R. Margules, Biological consequences of ecosystem fragmentation: a review, *Conservation Biology, 5*, 18-32, 1991.

Stephenson, A. G., The role of extrafloral nectaries of Catalpa speciosa in limiting herbivory and increasing fruit production, *Ecology, 63*, 663-669, 1982.

Stiles, G. F., Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species, *Ecology*, *56*, 285–301, 1975.

Stiles, G. F., Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest, *Science*, *198*, 1177-1178, 1977.

Stoner, K. E., Seasonal changes in abundance of tropical dry forest frugivorous and nectarivorous bats in northwestern Costa Rica, *Canadian Journal of Zoology, 79*, 1626-1633, 2001.

Stoner, K. E., O. Salazar, K. A., R. C. Fernández,, and M. Quesada Population dynamics, reproduction, and diet of the lesser long-nosed bat (*Leptonycteris curasoae)* in Jalisco, Mexico: implications for conservation, *Biodiversity and Conservation,* 12:357-373, 2003.

Stoner, K. E., M. Quesada, V. Rosas-Guerrero, and J. A. Lobo, Effects of forest fragmentation on Colima long-nosed bat foraging in tropical dry forest in Jalisco, Mexico, *Biotropica,* 34:462-467, 2003.

Tallak Nilsen, E., and W. H. Muller, Phenology of the drought-deciduous shrub *Lotus scoparius*: climatic controls and adaptive significance, *Ecological Monographs, 51*, 323–341, 1981.

Trejo, I., and R. Dirzo, Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico, *Biological Conservation, 94*, 133-142, 2000.

van der Meer, F., Physical Principals of Optical Remote Sensing, in *Spatial Statistics for Remote Sensing (Remote Sensing and Digital Image*

*Processing Vol, 1)*, edited by A. Stein, F. van der Meer, and B. Gorte, pp. 27-40, Kluwer Academic Publishers, New York, 1999.

van Schaik, C. P., Phenological changes in a Sumatran rain forest, *Journal of Tropical Ecology, 2,* 327–347, 1986.

van Schaik, C. P., J. W. Terborgh, and S. J. Wright, The phenology of tropical forests: Adaptive significance and consequences for primary consumers, *Annual Review of Ecology and Systematic, 24*, 353–377, 1993.

Walter, H., *Ecology of tropical and subtropical vegetation*, Oliver and Boyd, Edinburgh, 539 pp., 1971.

Williams-Linera, G., Phenology of deciduous and broad leaf evergreen tree species in a Mexican tropical lower montane forest, *Global Ecology and Biogeography Letters, 6*, 115-127, 1997.

Whitmore, T. C., and J. A. Sayer, Deforestation and species extinction in tropical moist forests, in *Tropical deforestation and species extinction*, edited by T. C. Whitmore and J. A. Sayer, pp. 1-14, Chapman and Hall, London, 1992.

Wright, S. J., Seasonal drought and the phenology of shrubs in a tropical moist forest, *Ecology*, *72*, 1643-1657, 1991.

Wright, S. J., and C. P. van Schaik, Light and the phenology of tropical trees, *The American Naturalist*, *143,* 192–199, 1994.

Wright, S. J., and F. H. Cornejo, Seasonal drought and leaf fall in a tropical forest, *Ecology 71,* 1165–1175, 1990.

Zimmerman, J. K., D. W. Roubik, J. D. Ackerman, Asynchronous phenology of a neotropical orchid and its euglossine bee pollinators, *Ecology, 70*, 1192–1195, 1989.

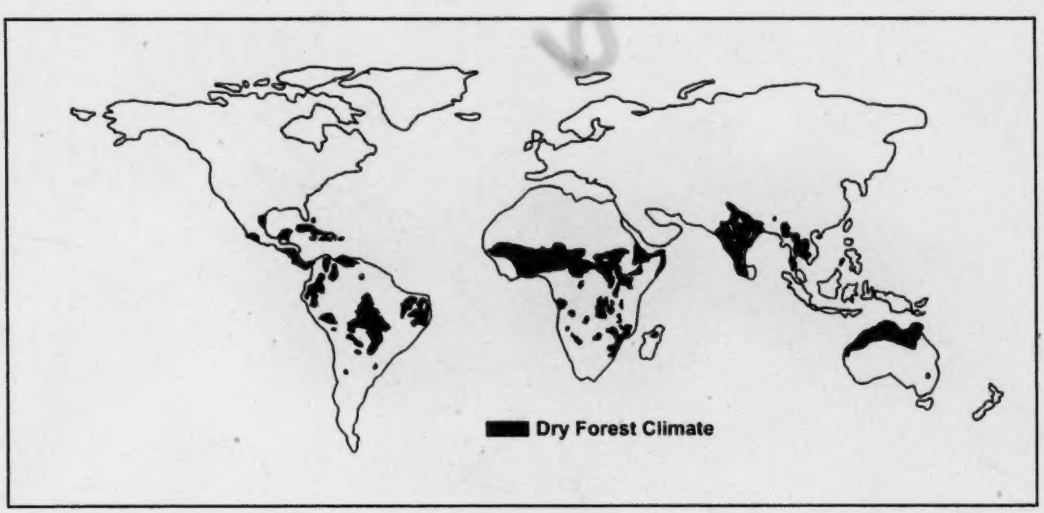
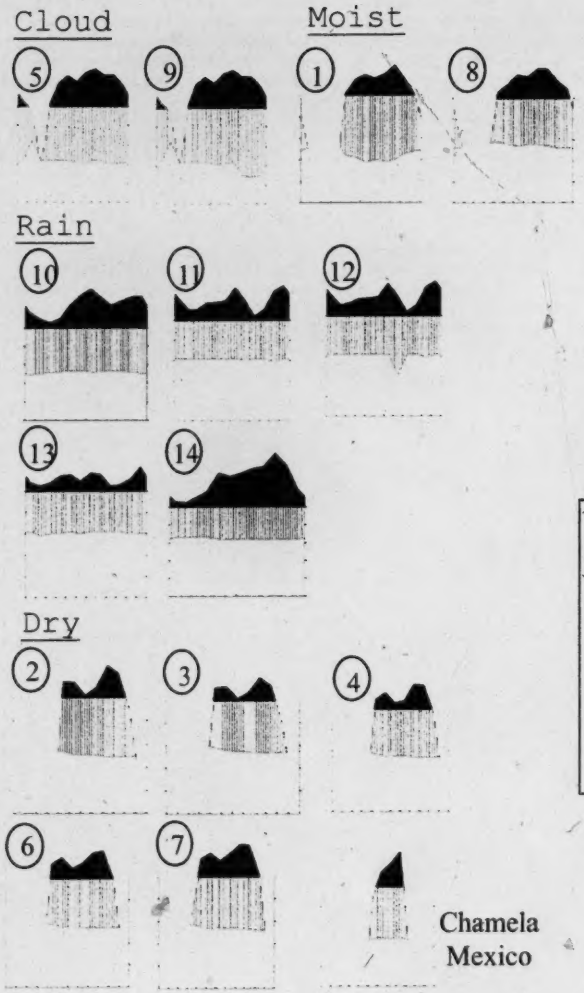
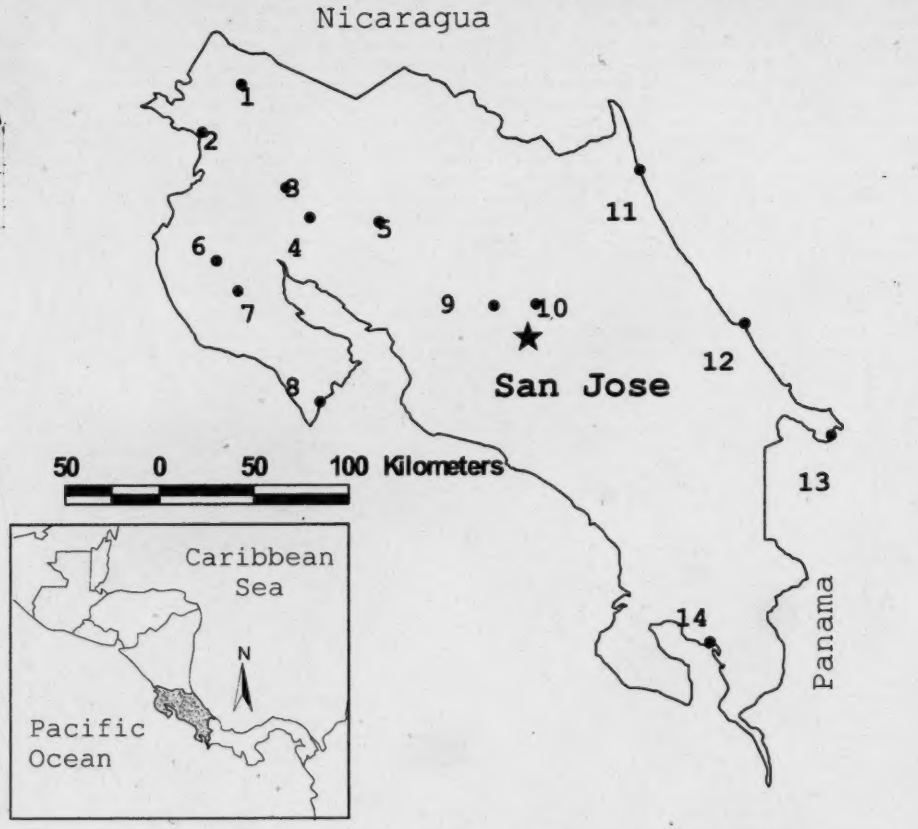



Figure 2.1. Areas around the world with a climate favorable for supporting a dry forest ecosystem. Spatial resolution: 0.5 degrees latitude by 0.5 degrees longitude (modified after Leemans 1992).




1 - Los Inocentes
2 - Santa Rosa
3 - Bagaces
4 - La Pacífica
5 - Monteverde
6 - Santa Cruz
7 - Nicoya
8 - Montezuma
9 - Poás Volcano
10 - La Selva
11 - Tortuguero
12 - Limón
13 - Sixaola
14 - Golfito

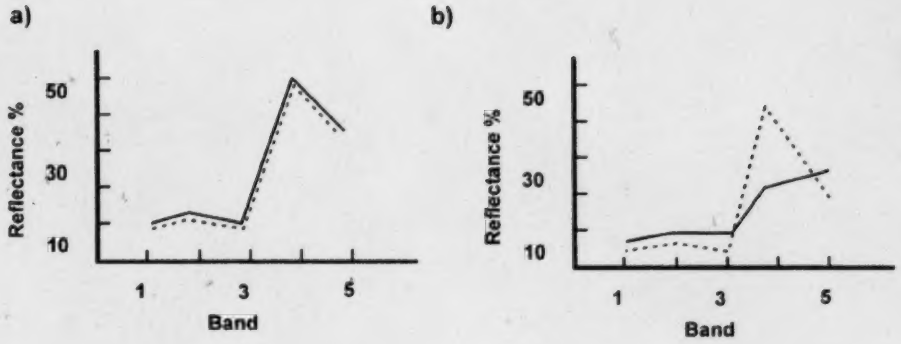



Figure 2.3. Spectral signatures of the dry forest at the Santa Rosa National Park from Landsat TM 5 images. a) wet season (October) and b) dry season (April). Solid line - deciduous forest, dashed line - evergreen forest.

### 3.1 Introduction

Tropical forests play an important role in international policies aimed at mitigating the effects of global climate change. One of the most important roles these forests play has been to sequester carbon (Birky 2001). Measures of carbon sequestration potential are used for developing carbon emissions reduction mechanisms in greenhouse gas emission policies (Pfaff et al. 2000). Generally, these mechanisms are integral to economic projections that provide estimations of how much carbon will be accumulated both with and without a carbon sequestration project (baseline). Baselines and the benefits of a given policy are often estimated from carbon sequestration models such as CENTURY (Metherell et al. 1996, Pan et al. 1998, Hilinski 2001, Pffaf et al. 2000). This model is one of the most robust and widely used biogeochemical models (Parton et al. 1987) used extensively to simulate biogeochemical cycles at regional to global scales (Pfaff et al. 2000). However, the effectiveness of these models in tropical environments is currently limited by the lack of accurate estimates of biophysical parameters such as Leaf Area Index (LAI), the area of foliage per area of ground. The forest plant production sub-model of CENTURY divides the trees into leaves, fine roots, fine branches, large wood, and coarse roots with carbon and nutrients allocated to the different plant parts. It is therefore, integral to the model to provide accurate estimates of LAI.

LAI is an especially important variable as it helps to understand energy and nutrient (water and carbon) exchange rates between the forest canopy and the

atmosphere (Fournier et al. 2003). LAI has been therefore used as the main variable in many growth and productivity models (Turner et al. 1999)

The prospect of accurately scaling up carbon sequestration estimates from the plot to the landscape level, using remote sensing approaches, has fuelled continued research to link spectral vegetation indices (SVI) derived from remotely sensed data to biophysical parameters such as LAI (Running et al. 1986, Turner et al. 1999, Fournier et al. 2003). Important linkages have been made with both empirical and physical LAI-SVI models with variable degrees of success (Hall et al. 1995).

SVIs in general extract information about a vegetated surface by exploiting differences in characteristic spectral regions of the reflected electromagnetic spectrum. One of the most commonly reported SVI in the literature and employed in regional/global monitoring systems is the Normalized Difference Vegetation Index (NDVI) (Running et al. 1986, Goward et al. 1991, Chen 1996). This index has been used to relate ground measurements such as LAI, biomass and chlorophyll to remotely sensed data and has one of the best-documented relationships to LAI (Tucker 1985, Turner et al. 2003). NDVI exploits the contrast in reflectance between the red and near infrared spectral bands. Vegetation strongly absorbs red wavelengths and highly reflects near infrared wavelength (Gates 1965, van der Meer 1999). The more vegetative biomass there is, the stronger the contrast is between these two spectral regions. It is by taking advantage of this spectral contrast, that NDVI can be related to leaf

properties (Verstraete and Pinty 1996). However, in linkages with LAI, NDVI has been found to saturate at LAI values between 3 and 8 (Birky 2001).

Much of the present research linking LAI with vegetation indices has been conducted on conifer stands (Running et al. 1986), agricultural crops (Asrar et al. 1984) and broad leaf forests in boreal and temperate environments (Chen and Cihlar 1995, White et al. 1997) with very promising results. Despite these significant efforts to develop techniques to quantify LAI and relate it to remotely sensed data in temperate and boreal ecosystems (Running et al. 1986, Running et al 1989, Price and Bausch 1995, Chen 1996, Chen and Cihlar 1996, Chen et al. 1997, White et al. 1997, Morrow and Friedl 1998, Qi et al. 2000, Thomas and Winne 2000, among others) there is a significant gap in similar research in tropical regions. Because the canopy architecture (horizontal and vertical structures) is different in tropical forests than in boreal or temperate forests, the methods developed in these ecosystems are not directly transferable to the tropics. For example, the issue of foliage clumping with branch and shoot architecture in conifer stands (Chen et al. 1997) is not an issue in tropical forests.

One problem with LAI estimations in tropical regions is that in general it is collected only for mature forests without consideration for the differences in canopy structure or composition found in secondary forest regeneration (Murphy and Lugo 1986, Weaver and Murphy 1990, Lean and Rowntree 1993), both of which have important effects on LAI. Because tropical forests exist in a spatial mosaic of successional stages that exhibit climatically induced compositional changes over relatively short geographic distances, such estimates of LAI are

inevitably inaccurate. Which, in turn lead to overestimations of canopy parameters at the landscape level.

The objectives of this study are to 1) document the variability of LAI in different stages of secondary growth in a tropical moist forest 2) explore functions that describe both the relationship and sensitivity of various SVIs to a range of LAI values, 3) evaluate the difference between a classical least squares regression model and a more robust nonparametric regression model for linking LAI to SVIs and 4) compare the performance of SVIs in temperate and boreal regions from previous studies to the performance of the same indices in a tropical environment.

### *3.1.1 Study Area*

The Basal Tropical Moist Forest (*Tm-f*) is both the most extensive and discontinuous life zone in Costa Rica (Janzen 1983). It is characterized by forest at an elevation of 0 – 1000m with a biotemperature >17°C and an average precipitation between 2000 – 4000mm per year (Holdridge 1967). At the mature stage, the *Tm-f* is comprised of tall (up to 50m) canopy trees, a multi-stratal (up to 3 strata) canopy and an abundance of vines and woody lianas (Janzen 1983).

The study area is located in NW Guanacaste, Costa Rica (11°01' N, 85° 30'W) at an elevation of 300-400 m (Figure 3.1a). The area is known as Los Inocentes. Our study area is located in the transition zone between the Basal Tropical Moist and Pre-Montane Tropical Moist Forests (Holdridge et al. 1971). Los Inocentes is a former 7 000 ha beef cattle ranch that was subsequently reduced to a 1 000 ha dairy cattle ranch and now serves as an eco-tourist lodge

and centre for conservation and ecological research. Adjacent to the Guanacaste Conservation Area, the Los Inocentes moist forest plays an important ecological role. Due to this location, it supports a complex array of flora and fauna that exhibits affinities of the dryer Pacific climate to the west, the wetter Atlantic climate to the east and the wetter cooler Lower Montane climate of the Central cordillera. The presence of plant species exhibiting three climatic affinities in one location confers considerable ecological interest on Los Inocentes.

Typical of many Central American tropical moist and dry forest zones, Los Inocentes suffered extensive deforestation during the middle decades of the last century. The land use / cover change process resulted in a forest habitat fragmented to the point of becoming shredded (Feinsinger 1997) wherein cattle pastures separate narrow corridors of riparian forests that border rivers and creeks. The riparian forest comprises of a mix of primary and secondary species (some of which are deciduous during the dry season). Transitions in land management practices over the years have resulted in extensive areas of cleared forest entering unmanaged regeneration. Some of these secondary forests began recovering immediately after clearing and now support successional forest up to 50 years of age.

In an extensive characterization of the area, Holdridge et al. (1971) reported that quaternary volcanic rocks such as andesite are dominant in the Los Inocentes region. Soils range from well to excessively well-drained reddish-brown latisols and lithosolic latisols. The surface layers are dark brown to

reddish-brown clay loam. Kaolinite is the dominant clay mineral with significant amounts of allophane and trace amounts of gibbsite.

## 3.2. Methods

### *3.2.1 Site Selection*

In March 2003, we selected nine forest sites of varying land use history on the Los Inocentes property (Figure 3.1b). In addition we selected three pastures (290 – 310m elevation) in different stages of regeneration on the property. The pastures represent a secondary forest in the earliest stages of regeneration. Therefore, for consistency in nomenclature we refer to the pasture sites as a 'very early' stage of regeneration. The random spatial distribution at all scales for the selected 12 sites was tested using Ripley's K function (Ripley 1976)

$$K(t) = (1/\text{intensity}) * E \qquad (1)$$

where 'intensity' is the mean number of points in a given area and E is the number of points at a distance less or equal to an arbitrary distance. Ripley's K function can summarize a point pattern or test a hypothesis about a spatial point pattern. It describes characteristics of the point processes at many distance scales (Freeman and Ford 2002). In many cases, data can have a combination of spatial patterns based on the scale (ex. clustered at small scales and random at large scales) (Diggle 1983). With Ripley's K function, these combinations can be seen. Our results indicate that all sites have a random spatial distribution at all scales between 0 and 1200m (Figure 3.2).

*3.2.2 Field Measurements*

*3.2.2.1 Structure and Composition*

At each site (forest and pasture) in a plot of 60 x 90m (0.54ha) we identified and measured the diameter-at-breast-height (DBH) of every tree and liana with a DBH > 5cm. We also measured the height of the six tallest trees (twice the number suggested by Holdridge 1967) in every forest site. In the pasture sites because there were less than six remnant trees, we measured the height of each.

*3.2.2.2. Definition of successional stages and description of selected sites*

In this paper we depart from the conventional use of "time (i.e. age) since abandonment" typical in remote sensing literature (Uhl et al. 1988, Lucas et al. 2001). We instead use the concept of "successional stages" because the structure of the regenerating forest is in part influenced by the time the area experienced anthropogenic disturbances (i.e. the length of time it was used as a pasture before abandonment) (Denslow 1996, Helmer 2002). Therefore, forest "age" alone may not be a reliable indicator of forest structure. Conventionally, forest age is characterized by the time elapsed since anthropogenic land use abandonment, being in many cases documented from local anecdotal evidence (Brondizio et al. 1996, Castro et al. 2002).

In contrast, successional stages provide better descriptions of secondary forest growth as seen in the horizontal and vertical structural planes (Montgomery and Chazdon 2001, Arroyo-Mora 2002). Therefore, successional stages eliminate problems associated with discrepancies arising from erroneous estimates of age

that preclude robust correlations with spectral vegetation indices. The twelve sample sites are distributed across four successional stages: very early (pasture), early, intermediate and late (Figure 3.4).

The very early stage is the most recently abandoned land. A thick inhibitory grass layer characterizes this stage along with a few emergent shrubs and remnant shade trees (Figure 3.4a). The dominant grasses are *Paspalum conjugatum* (Bergius) and *Hyparrhenia rufa* (Nees), 0.2 – 2.0m in height.

The early stage consists of stands of trees up to 10m tall with many emergent stems. The understory is dense with woody seedlings amid patches of *H. rufa* and *P. conjugatum* (Figure 3.4b). In this stage, lianas (ex. *Tetracera volubilis* (L.) and *Cissampelos pareira* (L.)) are present but are generally relatively thin although they can be found in large masses on more developed trees and along the edges that border pastures. The canopy is a single heterogeneous stratum with both many gaps and areas where the crowns of two or more trees overlap.

In the intermediate stage patches of *H. rufa* and *P. conjugatum* are no longer present (Figure 3.4c). While there are young seedlings present (height < 5m), the majority of the trees are taller (up to 15 - 20m) with a second canopy stratum beginning to develop. In all three sites there are patches of very dense foliage where there are multiple interlacing crowns. Gaps with emergent seedlings are still frequent as are areas where the foliage cover is relatively thin. Lianas (ex. *T. volubilis* and *Gouinia lupuloides* (L.) among others) are still present

and are thick in some areas. Most trees exhibit cylindrical trunks lacking buttresses.

In the late stage (Figure 3.4d) there are many large emergent trees with heights up to 45m. The canopy is thick and multistratal with the main upper canopy at heights greater than 25m. The understory has less light penetration than any other stage. Holdridge et al. (1971) found that at least 32 species became 30 m tall with a DBH of at least 50 cm. There are fewer woody seedlings, except in areas where there are gaps. Lianas (ex. *Philodendron* spp.) are generally only present in the upper canopy. Many of the larger trees are buttressed.

We analyzed the differences in physiognomic properties of the successional stages with a stepwise regression analysis in S+ using the physical measurements of height, basal area, density (number of stems) and number of species as predictors of successional stage. Also, to assess changes in ecosystem complexity we calculated the Holdridge Complexity Index (Holdridge 1967) from the variables of height (H), density of stems (D), number of species (S) and basal area (G):

$$C_{HCI} = \frac{H \times D \times S_p \times G}{1000} \qquad (2$$

Holdridge (1967) and Holdridge et al. (1971) originally used this index for mature forests only. However, Lugo et al. (1978) modified it for secondary forests. While the index and procedures are the same as the original $C_{HCI}$, all the trees

above 5cm DBH are included (instead of all trees above 10cm DBH). For this study, we adopted the modified $C_{HCI}$.

*3.2.2.3 Leaf Area Index*

Reliable estimates of LAI can be achieved from direct sampling methods, or optical measurements that have been calibrated by direct measurements such as point sampling (i.e. plumb bob), destructive sampling to construct allometric equations, or leaf litter traps (Ewel 1977, Lugo et al. 1978, Dufrêne and Bréda 1995, Vose et al. 1995, Liu et al. 1997, Thomas and Winne, 2000). For Los Inocentes these direct techniques cannot be implemented due to the species richness and the height of trees that can exceed 30m. Species density can reach 24-37 spp/0.1ha (Holdridge et al., 1971). For destructive sampling, trees in various stages of development of many species would have to be purchased and sampled, and the cost of such an endeavour is high both in terms of time and funds.

We measured effective LAI (LAIe) using a LAI-2000 Plant Canopy Analyzer (PCA) (Chen and Black 1991). The PCA is an optical instrument from Licor Inc. designed to derive the amount of radiation that penetrates the canopy. The sensor is composed of five concentric silicon rings with fields of view centered on 7°, 23°, 38°, 53° and 68° and receives sky radiation (<490nm to minimize scattering effects) through a hemispherical lens (Planchais and Pontailler 1999). Above canopy radiation (reference) measurements were taken both before and after each site. In addition, the sensor was fitted with a 45° view cap to eliminate the image of the operator. Values of LAIe were calculated from

the PCA using the readings only from the first four rings (Leblanc and Chen 2001). We assumed that the foliage was randomly oriented and therefore used the LAIe measurements as LAI values.

Spatially the measurements (insets of Figure 3.4) were taken according to a sampling scheme where the maximum surface area of the plots was covered without any overlap of the measurements. Because the area sampled by the PCA is largely dependent on the height of the canopy (LI-COR 1992), the spacing between measurements varied between successional stages. In each early plot we took 72 measurements, each covering a roughly triangular area of 10 x 14m. These LAI measurements cover 93% of the 0.54ha area. In each intermediate and late plot we took 12 measurements, each covering roughly a triangular area of 25 x 30m accounting for 83% of the surface area of the plots. In addition, in order to assess instrumental variation we assessed the variability in LAI calculations based on 1 to 10 readings of the same measurement. There was no significant variation (coefficient of variation = 0.005) in the estimate of LAI of the same triangular area in 1 to 10 measurements. Therefore, each of the 72 and 12 measurements per plot was taken in triplicate, with the average used in the LAI calculations.

We calculated descriptive statistics for the frequency distributions of the LAI measurements in each site and analyzed the presence of canopy gaps qualitatively using the second, third and fourth moments of the LAI frequency distributions. In addition, we analyzed differences in LAI as a function of successional stage with the Kruskal-Wallis and Mann-Whitney tests (Zar 1999,

Montgomery and Chazdon 2001). We also inferred the heterogeneity of the canopy by comparing the frequency distribution of each stage to its corresponding probability density function.

*3.2.3 Image Processing*

The satellite image used in this analysis is a Landsat 7 ETM+ image (28.5m spatial resolution) (Path 16, Row 52) acquired in June 2000. We orthorectified the image (using a 1:50,000 digital elevation model) to a Lambert Conformal Conic projection. The final root mean square error was less than 0.5 pixels in both the x and y directions. The digital number values were then converted to radiance to remove any bias due to sensor parameters (ACORN, 2001). Subsequently, we converted the radiance values to surface reflectance with the ACORN module in ENVI 3.4 using standard estimates of visibility and water vapour content. We elected to use surface reflectance rather than digital numbers, radiance or top of the atmosphere reflectance because past research has shown that surface reflectance is more sensitive to canopy structural properties (Huete et al. 1997). In addition, Turner et al. (1999) found surface reflectance optimal for establishing empirical LAI-SVI relationships. The reflectance values were extracted for a 3 x 3 pixel window (0.7ha) centred on the location of each field site. The coefficient of variation in these windows was generally less than 10%. We felt confident in using an image acquired in June when our field measurements were conducted in March because the forest is not caducifolious. The trees retain their leaves even in the dry season. The climate diagram in

Figure 3.3 illustrates that there is not an extended dry season, which would induce a dry deciduous leaf phenological pattern such as in the nearby dry forest in the Guanacaste Conservation Area (Figure 3.1a).

### *3.2.4 LAI-SVI Relationships*

We calculated five vegetation indices from the surface reflectance measurements using the red (band 3) and near-infrared (band 4) ETM+ bands: Simple Ratio (*SR*), Normalized Difference Vegetation Index (*NDVI*) (Rouse et al., 1974), Non-linear Index (*NLI*) (Goel and Qin, 1994), Modified Single Ratio (*MSR*) (Chen, 1996) and Soil Adjusted Vegetation Index 2 (*SAVI2*) (Qi et al., 1994). The formulas for these indices are listed in Table 3.1. We performed least-squares non-linear regression analyses (using transition functions) with TableCurve2D from Systat between LAI and the SVIs. However, since we recognize that neither LAI nor the SVIs are without error (Cohen et al. 2003, Fernandes et al. 2003) we performed a Theil-Sen regression (Theil 1950) in MatLab, which we compared to a least-squares regression on linearly transformed data in Mathematica.

In addition to analyzing the performance of the indices in the regression models, we illustrate a complete error calculation that takes into consideration the formula of the SVIs. Using standard rules of error propagation for arithmetic operations we derived error propagation formulas for each index.

## 3.3. Results

### *3.3.1 Structure and Composition*

We measured a total of 487 stems across 66 species (61 genera, 33 families) as listed in Table 3.2. While there is an overlap in species between stages, a gradual change in species composition can be inferred. We found a significant gradient in all the physiognomic parameters as well as the complexity index across the stages using a one-way ANOVA (Table 3.3).

In addition to the qualitative descriptions of the stages we developed a simple model to quantitatively describe the stages. We ran a stepwise regression with height, density and basal area. We did not include the number species in the development of the model for two reasons. First, it is difficult and very time consuming to accurately identify all the species, and second, the number of species is not strictly a structural characteristic but rather it is a measure of the number of ecological niches (Holdridge et al. 1971). The final model (0.19logD + 0.43logH - 0.35) is a combination of density (D) and height (H) ($F = 65.95$, $P < 0.001$, multiple $R^2 = 0.94$). Since the stages are not discrete entities but rather a continuum, the output of the model is the natural logarithm of a value between 1.0 and 4.0 where results closer to one (log values close to 0) are in an early stage of regeneration and closer to 4.0 (log values close to 1.4) are in a late stage of development.

### *3.3.2 Leaf Area Index*

The summary statistics for LAI per successional stage are presented in Table 3.4. The lowest standard deviation is observed for the very early stage ($k_1$ = 0.55), with a maximum of 1.96 for the late stage. Since the variances for the LAI data are not equal among the stages we used a non-parametric version of the one-way ANOVA the Kruskal-Wallis test to test if the population medians are different. Results from the Kruskal-Wallis test indicate that with an increase in forest maturity there is a simultaneous increase in LAI. The H value for the Kruskal-Wallis test is 91.4, indicating that the null hypothesis of "no differences between successional stages" can be rejected at the 0.05 significance level with a $\chi^2$ approximation of $P < 0.001$ (df = 3). Results from Mann-Whitney tests indicate that there is a significant difference in LAI values between all stages.

The values for skewness and kurtosis excess (Table 3.4) are not 0 and would therefore indicate that LAI values for each successional stage do not follow normal distributions. In this measure, kurtosis has been adjusted in such a way that a mesokurtic distribution (normal distribution about the mean) would have a value of 0 (Abell et al. 1998, Zar 1999, Wolfram 2000). The LAI values for all the stages show a positive skewness (indicating most values are low), with the exception of the intermediate stage, which is slightly negatively skewed (indicating most values are high). In an examination of the kurtosis coefficient (Table 3.4) the LAI data for the very early and early stages are leptokurtic (fewer values around $\mu-\sigma$ and $\mu+\sigma$ than a normal distribution) (Zar, 1999) and platykurtic for the intermediate and late stages. The most peaked distribution is seen for the very early stage ($k_3$ = 3.64) and the flattest as compared to a normal distribution is

in the mature stage ($k_3$ = -1.52). However, results from a D'Agostino-Pearson test (Table 3.4) indicate that the data from all of the stages except the very early are normal. The null hypothesis for this test is that the population is normal. If $H_0$ is rejected, a significant departure from symmetry or kurtosis or both is implied (Abell et al. 1998). However, the null hypothesis of the D'Agostino-Pearson test of a normal population can not be rejected because the values of skewness and kurtosis do not depart significantly from 0 (except for the very early stage).

When the frequency distribution of LAI for each stage is examined separately per stage (Figure 3.5) and (Figures 3.6a-d) information about the nature of the canopy and the distribution of the measurements falling into gaps vs. non-gaps can be inferred. In Figures 3.6a-d, the frequency distributions have been scaled to the probability density function with the same mean and standard deviation (smooth line).

*3.3.3 Red and Near- infrared reflectance*

In order to analyze the relationship between LAI and spectral vegetation indices (SVIs), we first examined the reflectance obtained from the Landsat 7 ETM+ image. The SVIs (Table 3.1) in this paper are calculated from Landsat band 3 ($\rho_r$) –red reflectance– and band 4 ($\rho_n$) –near infrared reflectance–. In Figure 3.7a, $\rho_r$ is plotted for the different successional stages. There is an observable trend of decreasing mean reflectance (8.6-2.7%) in the red portion of the spectrum as the forest matures. Figure 3.7b plots $\rho_n$ for the different stages. While there is an observable increase in mean reflectance from 28.1 to 44.4%, the

values reach a saturation plateau after the early stage. At the spatial resolution of Landsat (28.5m), the reflectance values will be determined by complex canopy interactions that are a combination of several inter-tree characteristics instead of individual plant characteristics. Our results for the Los Inocentes tropical moist forest follow the trend documented by Colwell (1974) showing a saturation of both the red and near infrared reflectance measurements at an LAI of approximately 3.5 (data not shown).

*3.3.4 Non-linear Regression*

The relationship between LAI and surface reflectance has been well documented in semiarid, temperate and boreal regions (Colwell 1974, Price and Bausch 1995, Kuusk 1998, Qi et al. 2000, Turner et al. 1999, Fernandes et al. 2003). Previous research indicates that vegetation indices have considerable sensitivity to changes in LAI, especially at lower LAI values (Chen 1996, Turner et al. 1999). Figures 3.8a-d illustrate the relationship between LAI and the four vegetation indices calculated in Table 3.1. The error bars represent one standard error. While the values for the indices are fairly well constrained, there is in general a larger variability in the corresponding LAI values. This is a result of the variation in the structure of the canopy as documented in this paper. A general trend of an increase in the indices with an increase in LAI is observed for each index. However, none of the indices have a linear relationship to LAI. In a non-linear regression analysis (Levenburg-Marquardt algorithm) of each index with LAI, we found that the relationship of LAI with each index is well represented by

a transition function (Lorentzian Cumulative) (Figure 3.9) where a = transition height; b = transition mid point and c = the half-width of the transition:

$$y = \frac{a}{\pi}\left(\arctan\left(\frac{x-b}{c}\right) + \frac{\pi}{2}\right) \quad (3)$$

The transition height (a) is the range of SVI values over which the index is sensitive to LAI in this environment. For example, the transition value for SR is 11.9 (Table 3.5). This means that SR has a range of 11.9 units in which it can detect changes in LAI. These values are not directly comparable between indices because they are specific to the range of values of each index. For example, NDVI is bound between –1 and 1 and therefore, the maximum value for the transition height is 2. The transition centre is the LAI value in the centre of the LAI range for which each SVI is sensitive and the transition half-width is half the range of LAI values to which each index is sensitive to without saturation.

The parameters of the best-fit Lorentzian Cumulative function for each SVI are listed in Table 3.5. The model has a good fit with each vegetation index: SR: F = 16.6, Adj. $R^2 = 0.78$, $P < 0.00$; MSR: F = 34.7, Adj. $R^2 = 0.84$, $P < 0.00$; SAVI2: F = 129.3, Adj. $R^2 = 0.97$, $P < 0.00$; NLI: F = 131.7, Adj. $R^2 = 0.97$, $P < 0.00$; NDVI: F = 115.5, Adj. $R^2 = 0.96$, $P < 0.00$.

### *3.3.5 Linear Regression*

In order to take into account the different errors in both LAI and the SVIs we performed two linear regressions. Errors inherent in the SVIs include

uncertainties in gaseous and water vapour absorption and relative calibration (Fernandes et al. 2003) as well as intra-site variability. In addition, these uncertainties are compounded by the error propagation through the calculation of each individual index (Table 3.6). Uncertainties in the LAI measurements are due to instrumental bias, differences in above and below canopy measurements as well as intra-plot heterogeneity. The total error values for the SVIs calculated from the formulas in Table 3.6 are listed in Table 3.7. These error values must be taken in the context of each index and cannot be directly compared.

As it is clear from the previous analysis that LAI does not have a linear relationship to the SVIs, for these two analyses, we log transformed LAI and the SVIs (except MSR which was reciprocally transformed) to produce a linear relationship. First, we ran ordinary linear squares regressions for each SVI and LAI. Next, in order to account for the errors we ran a Theil-Sen regression for each SVI and LAI (Theil 1950, Fernandes et al. 2003). The Theil-Sen regression is a robust structural regression that takes into account errors in both the dependent and independent variables (Fernandes et al. 2003). Table 3.8 and Figure 3.10 illustrate the results of the two models. The adjusted coefficient of determination is lower for each SVI with the Theil-Sen method but in addition, the $R^2$ for both linear models (classical and Theil-Sen) is lower than for the transition function models.

Because the values for the fit of the two linear regressions (classical and Theil-Sen) were close, we chose to do a stepwise linear regression (classical

model) with all the transformed SVIs. The final model included NDVI and NLI as the best predictors of LAI in a linear model ($F = 0.54.17$, $P < 0.001$, $R^2 = 0.92$).

## 3.4. Discussion

### *3.4.1 Leaf Area Index*

The large variation in LAI measurements, illustrated by the standard deviation ($k_l$= 0.55 - 1.96), indicates that the forest canopy is not homogeneous except in the very early stage of regeneration (grass canopy). The forest canopy in this tropical moist forest in different successional stages at Los Inocentes is a mosaic of gaps and canopy elements (leaves, branches, etc.) that do not form a spatially homogeneous cover in either the vertical or horizontal planes. Vertically, the number of forest strata differs per successional stage (Figures 3.4a-d). The presence of canopy members other than trees (i.e. lianas) also changes the vertical heterogeneity of the canopy. Thus, there are areas in the canopy that are naturally denser than others which in turn allow less light to penetrate and therefore, LAI values are higher in those areas. Horizontally, gaps may be present for many reasons such as tree falls. In addition, the number of overlapping canopies also alters the horizontal homogeneity.

Stages with large standard deviations (ex. early $k_l$ = 0.95) indicate that a variety of canopy conditions were sampled (Table 3.4). The minimum and maximum LAI values are also suggestive of a complex canopy structure. For example, in the early stage the mean LAI is 1.6, but the minimum and maximum values are 0.0 (gaps) and 3.8 (dense interlacing canopies), respectively. The box

and whisker plots in Figure 3.5 demonstrate the complexity of the *Tm-f* canopy. In all forest stages (excluding the very early stage) there is a large variation in LAI.

In the very early stage the variability is induced by the presence of remnant trees that were left to provide shade for the cattle and the horses that grazed in those areas while they were still pastures. The grass canopy is homogeneous compared to the tree canopies in the other stages. Because of the predominantly grass canopy the LAI is low (< 0.5). In the early stage, a large variability of LAI values is observed (0.0 – 3.8). The 5$^{th}$ and 95$^{th}$ percentiles (Figure 3.5) for this stage suggest that measurements were taken at points representing gaps (LAI = 0.0) and overlapping crowns (LAI = 3.8). The large variability in LAI is indicative of a spatially heterogeneous canopy. For the intermediate stage, some of the outliers (5$^{th}$ and 95$^{th}$ percentiles) in Figure 3.5 indicate measurements taken under single canopies (LAI = 2.0), while others were taken under a multi-stratal canopy (LAI = 4.2). While the LAI of this stage is significantly different from that of the early stage ($P$ = 0.00), there is a large overlap in the range of values. The symmetry about the mean as well as the fact that the 5$^{th}$ and 95$^{th}$ percentiles are closer to the 25$^{th}$ and 75$^{th}$ percentiles than in any of the other stages indicates a stable stage. Apart from certain species indicative of a mature forest, the intermediate stage is a mixture of both pioneer species and primary forest species. The late stage has the largest spread in the data; however, the range is between 3.7 and 10.9. There are fewer outliers and the majority of the LAI values fall within the 25$^{th}$ and 75$^{th}$

percentiles. However, the distance between the 25$^{th}$ and 75$^{th}$ percentiles is greater than for any of the other stages. This indicates that although the values of LAI are high, there is still a variability induced by the interlacing of the crowns and the different strata of the canopy. In addition, the late forest stage is a dynamic environment in which tree fall followed by rapid regeneration is common (Budowski 1965, Webb et al. 1972). Many secondary species begin to die to be replaced by species typical of a primary forest. For example three of the most common species in the intermediate stages, *Guazuma ulmifolia*, *Cordia alliodora* and *Gliricidia sepium* were not found in the late stage whereas species such as *Oxandra venezuelana, Platymiscium pinnatum* and *Manilkara chicle* not found in any other stage were more common in the late stage.

While overall an increase in the mean LAI can be observed between stages, the distribution of the data is also important to consider. Figure 3.6a depicts the very early stage where the majority of the measurements are around the mean (0.2). The few points in the range between 0.5-2.0 are therefore, responsible for the relatively large standard deviation in LAI for this stage. The measurements at these points were taken near remnant trees. In Figure 3.6b (early stage), more points were taken in less dense areas of the canopy. There are however, some points that fall into the higher range of LAI, which demonstrate the emergent variability of the regenerating forest canopy. However, as can be seen in Figure 3.6b, the LAI values with the greatest frequency in this stage are 1.0 - 2.0. The heterogeneity of this stage is exemplified when the full range of values is taken into consideration (0.0 – 3.8). Figure 3.6c (intermediate) indicates

a slightly less heterogeneous canopy, but outlying values are still observed. There is a probability of finding areas with low LAI values that can be attributed to areas with a lower foliage density. The majority of values fall closer to the mean ($k_2$ = -0.25) than in the early stage ($k_2$ = -0.37). The range of values for the late stage (Figure 3.6d) is wider than for the other forest stages ($k_1$= 1.96) indicative of a canopy with areas having up to three different strata. Overall, the values are greater because the forest is more developed and therefore, if there are gaps in the over story, the understory partially obscures them. In addition, this may be the result of a stand with low homogeneity with areas in which the trees have not reached their maximum survival age (Budowski 1965). There is a greater probability of finding areas with high LAI values, but there is also a large probability of encountering a site in which there are partial gaps.

### 3.4.2 *Regression analyses*

We recognize that no case can be made for either LAI or SVIs being measured without error, and therefore, least squares regression will provide attenuated values in the variance of the predicted variable (Cohen et al. 2003). However, because LAI is highly correlated with the SVIs (correlation > 0.8) the attenuation is a non-issue in this case. In addition, in this analysis we are not attempting to build a map of the LAI in the Los Inocentes region and therefore, in order to examine the relationship of LAI with the SVIs and to determine the range of LAI to which each is sensitive, least squares non-linear regression is applicable.

MSR with a range of sensitivity to LAI from 0.0 to 4.7 performed much better than any of the other indices. SR also performed marginally better than NDVI, SAVI2 or NLI with a range of sensitivity between 2.0 – 3.9. It however, is not useful for areas with LAI values below 2.0 or above 3.9. Both of these indices emphasize changes in the Red band rather than the near infrared. These results are consistent with what has been shown in other environments where LAI values are greater than 3 – 5 tend to saturate SVIs (Cohen et al. 2003). From Figure 3.9 it is clear that with few exceptions, single SVIs are not the optimal way to extract LAI where it is greater than 2.0. However, by using multiple indices, LAI can be categorized into broad ranges. For example, using SR early and intermediate stages can be distinguished from the late and the very early stages. And using NDVI, early stages can be distinguished from intermediate stages. The one exception is MSR, which is sensitive to changes in LAI values up to 4.7. However, in this tropical moist forest as in tropical wet forests (precipitation > 4000m/yr) where high LAI values are reached quickly during growth (Montomery and Chazdon 2000) other methods that are not hindered by the saturation of the red and near infrared reflectance need to be explored.

In order to assess the effect of different errors in LAI and the SVIs our results from the two linear regression techniques (Table 3.8) indicate that the Theil-Sen regression is more conservative in its fit. The differences between the two however, are minimal. The fit of the multiple regression is an improvement over the single regressions, including both NDVI and NLI. Nevertheless, Theil-Sen regression would be the more robust technique to use over classical least

squares if a linear model were to be used for modeling purposes. When the uncertainties for the SVIs are being calculated, the propagation of errors through the actual formula is an important component to consider (Table 3.7). It can be seen in Table 3.7 that certain SVIs (ex. SAVI2) have an unacceptably high uncertainty (+/-) compared to the actual index value once the error propagation is taken into consideration. For other SVIs (ex. NDVI) the uncertainty values are within an acceptable range.

An alternative to using multiple SVIs is to include tasseled cap indices such as greenness or wetness. Another possibility is the use of genetic algorithms. Fang et al. (2003) demonstrated very promising results in retrieving LAI from both field measured reflectance and Landsat ETM+ data. Their best result was $R^2 = 0.776$ with an RMSE of 1.064 using three genes. In a separate study, de Wasseige and Defourny (2003) showed similarly promising results in retrieving forest structure from bi-directional SPOT images. However, one technique yet to be explored, but with great potential for improving the retrieval of LAI from remotely sensed data are Bayesian Networks.

Another consideration in tropical environments that is a non-issue in temperate environments is the presence of lianas. In a pilot study in Panama, Sanchez-Azofeifa et al. (unpublished data) demonstrated that lianas have significantly higher reflectance (especially in the near infrared) than their respective host trees. This could be a problem in regional models because the ground LAI values may not reveal the increased reflectance values observed by

the sensors especially since lianas preferentially inhabit tree fall gaps (areas with low LAI).

### 3.5 Conclusions

- There is a significant gradient in LAI through the successional stages and a significant difference in LAI between the stages
- A Lorentzian Cumulative function best describes the relationships between the SVIs and LAI. It is a transition function that provides estimates of both the range of index sensitivity (transition height) and the range of LAI to which the index is sensitive (transition centre and transition width).
- Vegetation indices calculated from reflectance values showed expected trends when compared to field LAI data: increase with increasing LAI. The indices however became insensitive to LAI values above 2.0. The two exceptions to this were SR, which had sensitivity between 2.0 and 3.9, and MSR, which was sensitive from 0 up to 4.7.
- A linear least squares regression performed similarly to a more robust Theil-Sen regression, which accounts for the different errors in LAI and the SVIs. However, for large-scale models and LAI maps, the Theil-Sen technique is superior to the least squares.
- In the calculation of the errors associated with the SVI, it is not enough to only consider radiometric effects and intra-site variability. The errors are compounded by every arithmetic operation in the SVI formula and

therefore, the error propagation through the formula needs to be taken into consideration and used as the final uncertainty values. These all-inclusive uncertainty (+/-) values can then be used to choose the most useful SVIs for an analysis.

### 3.6 References


Abbell M.L., Braselton J.P., and Rafter J.A. 1998. Statistics with Mathematica. Academic Press, Toronto.

ACORN. 2001. ACORN Tutorial Version 3.12. Analytical Imaging and Geophysics.

Asrar G., Fuchs M., Kanemasu E.T., and Hatfield J.L. 1984. Estimating absorbed photosynthetic radiation and leaf area index from spectral reflectance of wheat. Agronomy Journal **76**:300-306.

Birky A. 2001. NDVI and a simple model of deciduous forest seasonal dynamics. Ecological Modelling **143**:43-58.

Brondizio E., Moran E., Mausel P., and Wu Y. 1996. Land cover in the Amazon Estuary: Linking of the Thematic Mapper with botanical and historical data. Photogrammetric Engineering and Remote Sensing **62**:921-929.

Budowski G. 1965. Distribution of Tropical American rainforest species in the light of successional processes. Turrialba **15**:40-42.

Castro K.L., Sanchez-Azofeifa G.A., and Rivard B. 2003. Monitoring secondary tropical forests using space-borne data: implications for Central America. International Journal of Remote Sensing. **24**:1853-1874.

Chen J.M., and Black T.A. 1991. Measuring leaf area index of plant canopies with branch architecture. Agricultural and Forest Meteorology **57**:1-12.

Chen J.M., and Cihlar J. 1995. Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. IEEE Transactions on Geoscience and Remote Sensing **33**:777-787.

Chen J.M. 1996. Evaluation of vegetation indices and a modified simple ratio for Boreal applications. Canadian Journal of Remote Sensing **22**:229-241.

Chen J.M., Rich P.M., Gower S.T., Norman J.M., and Plummer S. 1997. Leaf area index of boreal forests: Theory, techniques and measurements. Journal of Geophysical Research **102**:24429-24443.

Cohen W.B., T. K. Maiersperger, Gower S.T., and Turner D.P. 2003. An improved strategy for regression of biophysical variables and Landsat ETM+ data. Remote Sensing of Environment **84**:561-571.

Colwell J. 1974. Vegetation canopy reflectance. Remote Sensing of Environment **3**:175-183.

de Wasseige C., and Defourny P. 2002. Retrieval of tropical forest structure characteristics from bi-directional reflectance of SPOT images. Remote Sensing of Environment **83**:362-375.

Denslow J. 1996. Functional group diversity and responses to disturbance. *in* Orians G. and et al., editors. Biodiversity and Ecosystem Processes in Tropical Forest. Springer.

Diggle P.J. 1983. Statistical Analysis of spatial point patterns. Academic Press, NewYork.

Dufrene E., and Breda N. 1995. Estimation of deciduous forest leaf area index using direct and indirect methods. Oecologia **104**:156-162.

Ewel J.J. 1977. Differences between wet and dry successional tropical ecosystems. Geo-Eco-Trop **1**:103-117.

Fang H., Liang S., and Kuusk A. 2003. Retrieving leaf area index using a genetic algorithm with a canopy radiative transfer model. Remote Sensing of Environment **85**:257-270.

Feinsinger P. 1997. Habitat Shreding. *in* G. K. Meffe and C. R. Carroll, editors. Principles of Conservation Biology. Sinauer Associates, Massachusetts.

Fernandes R.F., Butson C., Leblanc S.G., and Latifovic R. 2003. Landsat-5 TM and Landsat-7 ETM+ based accuracy assessment of leaf area index products for Canada derived from SPOT-4 VEGETATION data. Canadian Journal of Remote Sensing **29**:241-258.

Freeman E.A., and Ford E.D. 2002. Effects of data quality on analysis of ecological pattern using the K(d) statistical function. Ecology **83**:35-46.

Fournier R.A., Mailly D., Walter J.-M.N., and Soudani K. 2003. Measurement of Forest Structure. *in* Wulder M. and Franklin S, editors. Methods for Remote Sensing of Forests: Concepts and Case Studies. Kluwer Academic Press.

Goel N.S., and Qin W. 1994. Influences of canopy archtecture on relationships between various vegetation indices and LAI and FPAR: a computer

simulation. Remote Sensing Reviews **10**:309-347.

Goward S.N., Markham B., Dye D.G., Dualney W., and Yand J. 1991. Normalized difference vegetation index measurements for the Advanced Very High Resolution Radiometer. Remote Sensing of Environment **35**:257-277.

Haase, P. 2000. *Ecological Climate Diagram (ECD) Program Version 1.0.* http://home.t-online.de/home/haasep/frm_ecd.htm (Last accessed: July 6, 2003).

Hall F.G., Townshend J.R., and Engman E.T. 1995. Status of remote sensing algorithms for estimation of land surface state parameters. Remote Sensing Environment **51**:138-156.

Helmer E.H., Brown S., and Cohen W.B. 2000. Mapping montane tropical forest successional stages and land use with multi-date Landsat Imagery. International Journal of Remote Sensing **21**:2163-2183.

Hilinski T. 2001. Century Soil Organic Matter Model. Version 5. User's Guide and Reference. Natural Resource Ecology Laboratory, Colorado State University.

Holdridge L. 1967. Life Zone Ecology. Tropical Science Center, San Jose, Costa Rica.

Holdridge L., Grenke W.C., Hatheway W.H., Liang T., and Tosi J.Jr. 1971. Forest Environments in Tropical Life Zones: A Pilot Study. Pergamon Press, New York.

Huete A.R., Liu H.Q., Batchily K., and van Leeuwen W. 1997. A comparison of

vegetation indices over a global set of TM Images for MODIS-EOS. Remote Sensing Environment **59**:440-451.

Janzen D.H., editor. 1983. Costa Rican Natural History. University of Chicago Press, Chicago.

Kuusk A. 1998. Monitoring vegetation parameters on large areas by the inversion of a canopy reflectance model. International Journal of Remote Sensing **19**:2983-2905.

Lean J., and Rowntree P.R. 1993. GCM simulation of the impact of Amazonian deforestation on climate using an improved canopy representation. Quarterly Journal of the Royal Meteorological Society **119**:509-530.

Leblanc S., and Chen J.M. 2001. A practical scheme for correcting multiple scattering effects on optical LAI measurements. Agricultural and Forest Meteorology **110**:125-139.

LI-COR Inc. 1992. LAI-2000 Plant Canopy Analyzer Instruction/Operating Manual. LI-COR Inc., Lincoln NE.

Liu S., Riekerk H., and Gholz H.L. 1997. Leaf litter fall, leaf area index and radiation transmittance in cypress wetlands and slash pine plantations in north-central Florida. Wetlands Ecology and Management **4**:257-271.

Lucas R.M., Honzak J., Curran P.J., Foody G.M., Milnes R., Brown T., and Amral S. 2000. Mapping the regional extent of tropical forest regeneration stages in the Brazilian Legal Amazon using NOAA-AVHRR data. International Journal of Remote Sensing **21**:2855-2881.

Lugo A.E., Gonzalez-Liboy J.A., Cintron B., and Dugger K. 1978. Structure,

productivity and transpiration of a subtropical dry forest in Puerto Rico. Biotropica **10**:278-291.

Metherell A.K., Harding L.A., Cole C.V., and Parton W.J. 1996. CENTURY soil organic matter model environment. Technical Report No. 4 USDA-ARS Great Plains System Research Unit, Fort Collins.

Montgomery R.A., and Chazdon R.L. 2001. Forest structure, canopy architecture and light transmittance in tropical wet forests. Ecology **82**:2707-2718.

Morrow N., and Friedl M.A. 1998. Modeling biophysical controls on land surface temperature and reflectance in grasslands. Agricultural and Forest Meteorology **92**:147-161.

Murphy P.G., and Lugo A.E. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica **18**:89-96.

Pan Y.D., Melillo J.M., McGuire A.D., Kicklighter D.W., Pitelka L.F., Hibbard K., Pierce L.L., Running S.W., Ojima D.S., Parton W.J., and Schimel D. 1998. Modeled responses of terrestrial ecosystems to elevated atmospheric CO2: A comparison of simulations by the biogeochemistry models of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). Oecologia **114**:389-404.

Parton W.J., Schimel. D.S., Cole C.V., and Ojima D.S. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal **51**:1173-1179.

Pfaff A.S.P., Kerr S., Hughes F., Liu S., Sanchez-Azofeifa G.A., Schimel D., Tosi J., and Watson V. 2000. The Kyoto protocol and payments for tropical

forests: An interdisciplinary method for estimating carbon-offset supply and increasing the feasibility of a carbon market under the CDM. Ecological Economics **35**:203-221.

Planchais I., and Pontailler J.-Y. 1999. Validity of leaf areas and angles estimated in a Beech forest from analysis of gap frequencies, using hemispherical photographs and a plant canopy analyzer. Annals of Forest Science **56**:1-10.

Price J.C., and Bausch W.C. 1995. Leaf area index estimates from visible and near infrared reflectance data. Remote Sensing of Environment **52**.

Qi J., Kerr Y.H., Moran M.S., Weltz M., Heute A.R., and Sorooshian S. 1994. A soil modified adjusted vegetation index. Remote Sensing of Environment **48**:118-126.

Ripley D. 1976. The second-order analysis of stationary point processes. Journal of applied probability **13**:255-266.

Rouse J.W., Hass R.H., Shell J.A., and Deering D.W. 1974. Monitoring vegetation systems in the Great Plains with ERTS-1. Pages 309-317 *in* Third Earth Resources Technology Satellite Symposium.

Running, S. W., R. R. Nemani, Peterson D.L., L. E. Band, D. F. Potts, L. L. Pierce, and M. A. Spanner. 1989. Mapping regional forest evapotranspiration and photosynthesis by coupling satellite data with ecosystem simulation. Ecology **70**:1090-1101.

Running S.W., Peterson D.L., Spanner M.A., and Teuber K.B. 1986. Remote sensing of coniferous forest leaf area. Ecology **67**:273-276.

Theil H. 1950. A rank-invariant method of linear and polynomial regression analysis. Netherlands Academy of Science, Series A **53**:386-392.

Thomas S.C., and Winne W.E. 2000. Leaf area index of an old-growth Douglas-fir forest established from direst structural measurements in the canopy. Canadian Journal of Forest Resources **30**:1922-1930.

Tucker C.J. 1985. Satellite remote sensing of total herbaceous biomass production in the Senegalese Sahel: 1980-1984. Remote Sensing of Environment **17**:233-249.

Turner D.P., Cohen W.B., Kennedy R.E., Fassnacht K.S., and Briggs J.M. 1999. Remote Sensing of Environment **70**:52-68.

Uhl C., Buschbacher R., and Serrao E.A.S. 1988. Abandoned pastures in Eastern Amazonia. I. Patterns of plant succession. Journal of Ecology **76**:663-681.

van der Meer F. 1999. Physical Principles of Optical Remote Sensing. Pages 27-40 *in* Stein A., van der Meer F., and Gorte B., editors. Spatial Statistics for Remote Sensing. Kluwer Academic Press, Dordrecht, The Netherlands.

Verstraete M.M., and Pinty B. 1996. Designing optimal spectral indexes for remote sensing applications. IEEE Transactions on Geoscience and Remote Sensing **34**:1254-1265.

Vose J.M., Sullivan N.H., Clinton B.D., and Bolstad P.V. 1995. Vertical leaf area distribution, light transmittance and application of the Beer-Lambert law in four mature hardwood stands in the southern Appalachians. Canadian Journal of Forest Resources **25**:1036-1043.

Weaver P.L., and Murphy P.G. 1990. Forest structure and productivity in Puerto

Rico's Luquillo Mountains. Biotropica **22**:69-82.

Webb L.J., Tracey J.G., and Williams W.T. 1972. Regeneration and pattern in the subtropical rain forest. Journal of Ecology **60**:675-695.

White J.D., Running S.W., Ramakrishna N., Keane R.E., and Ryan K.C. 1997. Measurement and remote sensing of LAI in Rocky Mountain montane ecosystems. Canadian Journal of Forest Resources **27**:1714-1727.

Wolfram S. 2000. The Mathematica Book, Fourth Edition. Wolfram Research, Champaign, IL.

Zar J.H. 1999. Biostatistical Analysis, Fourth Edition. Prentice Hall, New Jersey, USA.

Table 3.1. Formulas for the four vegetation indices used in the analysis

Vegetation Index Formulas

$$NDVI = \frac{(\rho_n - \rho_r)}{(\rho_n + \rho_r)}$$

$$NLI = \frac{(\rho_n^2 - \rho_r)}{(\rho_n^2 + \rho_r)}$$

$$MSR = \frac{\frac{\rho_n}{\rho_r} - 1}{\sqrt{\frac{\rho_n}{\rho_r} + 1}}$$

$$SAVI2 = \rho_n + 0.5 - \sqrt{(\rho_n + 0.5)^2 - 2 \times (\rho_n - \rho_r)}$$

$$SR = \frac{\rho_n}{\rho_r}$$

*$\rho_3$ = red reflectance, $\rho_4$ = near infrared reflectance

Table 3.2. List of species inventoried (DBH > 5cm) in sample plots at Los Inocentes. There are a total of 33 Families, 61 genera and 66 species in this inventory. Pasture – 4 spp., Early – 8 spp., Intermediate – 31 spp., Late – 40 spp.

| Family | Species | Pasture | Early | Intermediate | Late |
|---|---|---|---|---|---|
| Anacardiaceae | *Tapirira myriantha* (Triana & Planch) | | | x | x |
| Annonaceae | *Oxandra venezuelana* (R.E.Fr.) | | | | x |
| | *Xylopia frutescens* (Aubl) | | | | x |
| Apocynaceae | *Stemmadenia obovata* (Hook. & Arn.) | | | x | x |
| Arecaceae | *Acrocomia aculeata* (Jacq.) | x | | x | |
| Asteraceae | *Vernonia patens* (Kunth.) | | x | | |
| Bignonaceae | *Tabebuia chrysantha* (Jacq.) | | | x | x |
| | *Tabebuia ochracea* (Cham.) | | | x | x |
| | *Tabebuia rosea* (Bertol.) | x | x | x | |
| Bombacaceae | *Quararibea funebris* (La Llave) | | | | x |
| Boraginaceae | *Cordia alliodora* (Ruiz & Pav.) | x | | x | |
| | *Cordia collococca* (L.) | | | x | |
| | *Cordia dentate* (Poir) | | | x | |
| Burseraceae | *Bursera simaruba* (L.) | | | x | |
| | *Tetragastris panamensis* (Engl.) | | | | x |
| Cecropiaceae | *Cecropia peltata* (L.) | | | x | |
| Clusiaceae | *Clusia rosea* (Jacq.) | | | | x |
| | *Garcinia intermedia* (Pittier) | | | | x |
| Combretaceae | *Terminalia oblonga* (Ruiz & Pav) | | | | x |
| Euphorbiaceae | *Croton schiedeanus* (Schltdl) | | | | x |
| | *Sapium glandulosum* (L.) | | x | x | |
| Fabaceae - Caesalpinoideae | *Dialium guianense* (Aubl.) | | | | x |
| | *Hymenaea courbaril* (L.) | | | | x |
| Fabaceae - Mimosoidea | *Acacia collinsi* (Saff.) | | | x | |
| | *Albizia adinocephala* (Donn.Sm.) | | | x | |
| | *Cojoba arborea* (L.) | | | | x |
| | *Enterolobium cyclocarpum* (Jacq.) | x | x | x | |
| | *Inga vera* (Willd) | | | | x |
| | *Samanea saman* (Jacq.) | | x | x | |
| Fabaceae - Papilionoideae | *Diphysa Americana* (Mill.) | | | x | |

| | | | | |
|---|---|---|---|---|
| | *Gliricidia sepium* (Jacq.) | x | x | |
| | *Lonchocarpus felipei* (N. Zamora) | | x | |
| | *Myroxylon balsamum* (L.) | | | x |
| | *Ormosia coccinea* (Aubl.) | | | x |
| | *Piscidia carthagenensis* (Jacq.) | | x | x |
| | *Platymiscium pinnatum* (Jacq.) | | | x |
| | *Pterocarpus michelianus* (N. Zamora) | | | x |
| Flacourtiaceae | *Laetia procera* (Poepp.) | | | x |
| Lauraceae | *Cinnamomum brenesii* (Standl.) | | x | |
| | *Persea americana* (Mill.) | | x | |
| Malpighiaceae | *Byrsonima crassifolia* (L.) | | x | |
| Melastomataceae | *Miconia argentea* (Sw.) | | x | |
| Meliaceae | *Guarea bullata* (Radlk.) | | | x |
| | *Guarea pterorhachis* (Harms.) | | | x |
| | *Swietenia macrophylla* (King) | | | x |
| Moraceae | *Brosimun alicastrum* (Sw.) | | | x |
| | *Castilla elastica* (Sesse) | | | x |
| Myristicaceae | *Virola koschnyi* (Ward) | | | x |
| Myrtaceae | *Psidium guajava* (L.) | | x | |
| Olacaceae | *Heisteria acuminata* (Humb. & Bonpl.) | | | x |
| Rhizophoraceae | *Cassipourea guianensis* (Aubl.) | | | x |
| Rubiaceae | *Morinda panamensis* (Seem.) | | x | |
| Rutaceae | *Esenbeckia pentaphylla* (Macfad.) | | | x |
| | *Zanthoxylum setulosum* (P. Wilson) | x | x | x |
| Sapindaceae | *Cupania rufescens* (Triana & Planch.) | | | x |
| | *Dilodendron costaricense* (Radlk.) | | | x |
| | *Matayba oppositifolia* (A. Rich.) | | | x |
| Sapotaceae | *Chrysophyllum brenesii* (Cronquist) | | | x |
| | *Manilkara chicle* (Pittier) | | | x |
| | *Pouteria sp* | | | x |
| Simaroubaceae | *Simarouba glauca* (DC.) | | | x |
| Sterculiaceae | *Guazuma ulmifolia* (Lamarck) | x | x | |
| Tiliaceae | *Apeiba tibourbou* (Aubl.) | | x | |
| | *Luehea seemannii* (Triana & Planch.) | | x | |
| Verbenaceae | *Vitex cooperi* (Standl.) | | x | |
| Vochysiaceae | *Vochysia guatemalensis* (Donn. Sm.) | | | x |

Table 3.3 Mean values with one standard deviation of the forest structural characteristics along with the Holdridge Complexity Index; a measure of forest physiognomy.

| Stage | Height | Basal Area | Density | Species | HCI |
|---|---|---|---|---|---|
| Very early | 6.3±0.6 | 4.7±7.1 | 3±3 | 2±1 | 0.1±0.1 |
| Early | 6.7±0.6 | 11.2±8.4 | 27±9 | 4±3 | 1.4±1.8 |
| Intermediate | 14.0±1.7 | 27.6±3.7 | 76±22 | 11±6 | 40.5±28.9 |
| Late | 30.0±1.0 | 38.4±9.3 | 48±17 | 18±6 | 112.9±75.6 |

*Height is measured in meters, basal area in $m^2$/hectare, density in number of stems and species as the number of species. HCI is unit less.

Table 3.4. Summary statistics for LAI in the different successional stages.

| Stage | Min | Max | M | $k_1$ | $k_2$ | $k_3$ | D'A.-P | *P* |
|---|---|---|---|---|---|---|---|---|
| Very early | 0.0 | 2.0 | 0.22 | 0.55 | 2.27 | 3.65 | 35.7 | <0.00 |
| Early | 0.0 | 3.8 | 1.65 | 0.95 | 0.39 | 0.39 | 1.9 | 0.38 |
| Intermediate | 2.0 | 4.8 | 3.20 | 0.82 | -0.25 | -1.52 | 2.0 | 0.36 |
| Late | 3.7 | 10.9 | 6.90 | 1.96 | 0.31 | -0.38 | 0.6 | 0.75 |

* $\mu$ = mean, $k_1$ = standard deviation, $k_2$ = skewness, $k_3$ = kurtosis excess, D'A.-P. = D'Agostino-Pearson test for departure from normality test statistic, *P* = p-value for D'Agostino - Pearson test.

Table 3.5. Parameters of Best-Fit Lorentzian Cumulative Models for the LAI-SVI relationship.

| Y | TH | $P_{th}>\|t\|$ | TW | $P_{tw}>\|t\|$ | TC | $P_{tc}>\|t\|$ | $R^2$ |
|---|---|---|---|---|---|---|---|
| SR | 11.9 | 0.01 | 1.96 | 0.36 | 2.89 | 0.00 | 0.78 |
| NDVI | 0.36 | 0.00 | 0.90 | 0.03 | 1.50 | 0.00 | 0.96 |
| NLI | 0.02 | 0.00 | 0.74 | 0.12 | 1.19 | 0.00 | 0.97 |
| SAVI2 | 0.25 | 0.00 | 0.84 | 0.03 | 1.45 | 0.00 | 0.97 |
| MSR | 8.26 | 0.00 | 4.68 | 0.01 | 2.34 | 0.01 | 0.84 |

*TH = transition height, TW = transition width, TC=transition centre, $R^2$ = Adjusted coefficient of determination

Table 3.6. Formulas for the propagation errors through the vegetation indices. Formulas derived from the standard rules of error propagation in arithmetic operations.

Vegetation index error terms

$$\delta NDVI = \alpha\left(\frac{\delta\rho_n + \delta\rho_r}{Abs[\rho_n - \rho_r]} + \frac{\delta\rho_n + \delta\rho_r}{Abs[\rho_n + \rho_r]}\right)$$

$$\delta NLI = \alpha\left(\frac{\delta\rho_n + \delta\rho_r}{\rho_n^2 - \rho_r} + \frac{\delta\rho_n + \delta\rho_r}{\rho_n^2 + \rho_r}\right)$$

$$\delta SAVI2 = \frac{\left(2(\delta\rho_n + \delta\rho_r) + \frac{2\delta\rho_n\, Abs[0.5+\rho_n]^2}{0.5+\rho_n}\right)\sqrt{Abs[(0.5+\rho_n)^2 - 2(\rho_n - \rho_r)]}}{2((0.5+\rho_n)^2 - 2(\rho_n - \rho_r))}$$

$$\delta MSR = \alpha\left(\frac{\delta\rho_n}{Abs[\rho_n]} + \frac{\delta\rho_r}{Abs[-1+\rho_r]} + \frac{\sqrt{Abs\left[\frac{\rho_n}{1+\rho_r}\right]}\left(\frac{\delta\rho_n}{Abs[\rho_n]} + \frac{\delta\rho_r}{Abs[1+\rho_r]}\right)}{2\sqrt{\frac{\rho_n}{1+\rho_r}}}\right)$$

$$\delta SR = \alpha\left(\frac{\delta\rho_n}{Abs\rho_n} + \frac{\delta\rho_r}{Abs\rho_r}\right)$$

*$\alpha$ = value of vegetation index (i.e. NDVI), $\rho_n$ = near infrared reflectance, $\rho_r$ = red reflectance.

Table 3.7 Mean SVI values and total error values for each vegetation index calculated from the formulas in Table 3.6.

| Plot | Stage | μSAVI | δSAVI2 | μNLI | δNLI | μNDVI | δNDVI | μMSR | δMSR | μSR | δSR |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | VE | 0.72 | 1.13 | 0.98 | 0.07 | 0.68 | 0.04 | 2.38 | 0.23 | 5.33 | 0.24 |
| 2 | VE | 0.70 | 1.48 | 0.97 | 0.10 | 0.66 | 0.04 | 2.27 | 0.27 | 4.96 | 0.27 |
| 3 | VE | 0.69 | 3.61 | 0.97 | 0.25 | 0.53 | 0.08 | 2.15 | 0.27 | 3.26 | 0.29 |
| 4 | E | 0.87 | 2.18 | 0.99 | 0.10 | 0.77 | 0.06 | 4.01 | 0.69 | 7.93 | 0.91 |
| 5 | E | 0.85 | 2.42 | 0.99 | 0.12 | 0.74 | 0.06 | 3.47 | 0.51 | 6.76 | 0.64 |
| 6 | E | 0.79 | 0.88 | 0.99 | 0.04 | 0.65 | 0.02 | 2.63 | 0.08 | 4.86 | 0.10 |
| 7 | I | 0.88 | 4.10 | 0.99 | 0.18 | 0.78 | 0.10 | 4.30 | 1.10 | 8.34 | 1.45 |
| 8 | I | 0.90 | 0.61 | 0.99 | 0.03 | 0.82 | 0.02 | 5.06 | 0.23 | 10.71 | 0.28 |
| 9 | I | 0.93 | 1.96 | 0.99 | 0.10 | 0.87 | 0.05 | 7.02 | 0.58 | 15.31 | 0.78 |
| 10 | L | 0.93 | 2.19 | 0.99 | 0.10 | 0.87 | 0.53 | 7.58 | 0.10 | 15.02 | 1.27 |
| 11 | L | 0.93 | 2.23 | 0.99 | 0.10 | 0.87 | 0.05 | 7.01 | 0.89 | 14.69 | 1.09 |
| 12 | L | 0.92 | 1.60 | 0.99 | 0.08 | 0.85 | 0.04 | 6.16 | 0.51 | 12.82 | 0.63 |

Table 3.8 Best-Fit Theil-Sen and linear Least Squares Models with adjusted $R^2$ values

| Y | Theil-Sen Model | $R^2$ | Least Squares Model | $R^2$ |
|---|---|---|---|---|
| SR | 0.4129x+0.8189 | 0.77 | 0.3477x+0.8388 | 0.80 |
| NDVI | 0.1046x-0.1453 | 0.79 | 0.1022x-0.1436 | 0.79 |
| MSR | -0.1982x+0.3053 | 0.75 | -0.1674x+0.2937 | 0.77 |
| SAVI | 0.0736x-0.0888 | 0.69 | 0.0618x-0.0816 | 0.73 |
| NLI | 0.0045x-0.0046 | 0.62 | 0.0037x-0.0042 | 0.66 |

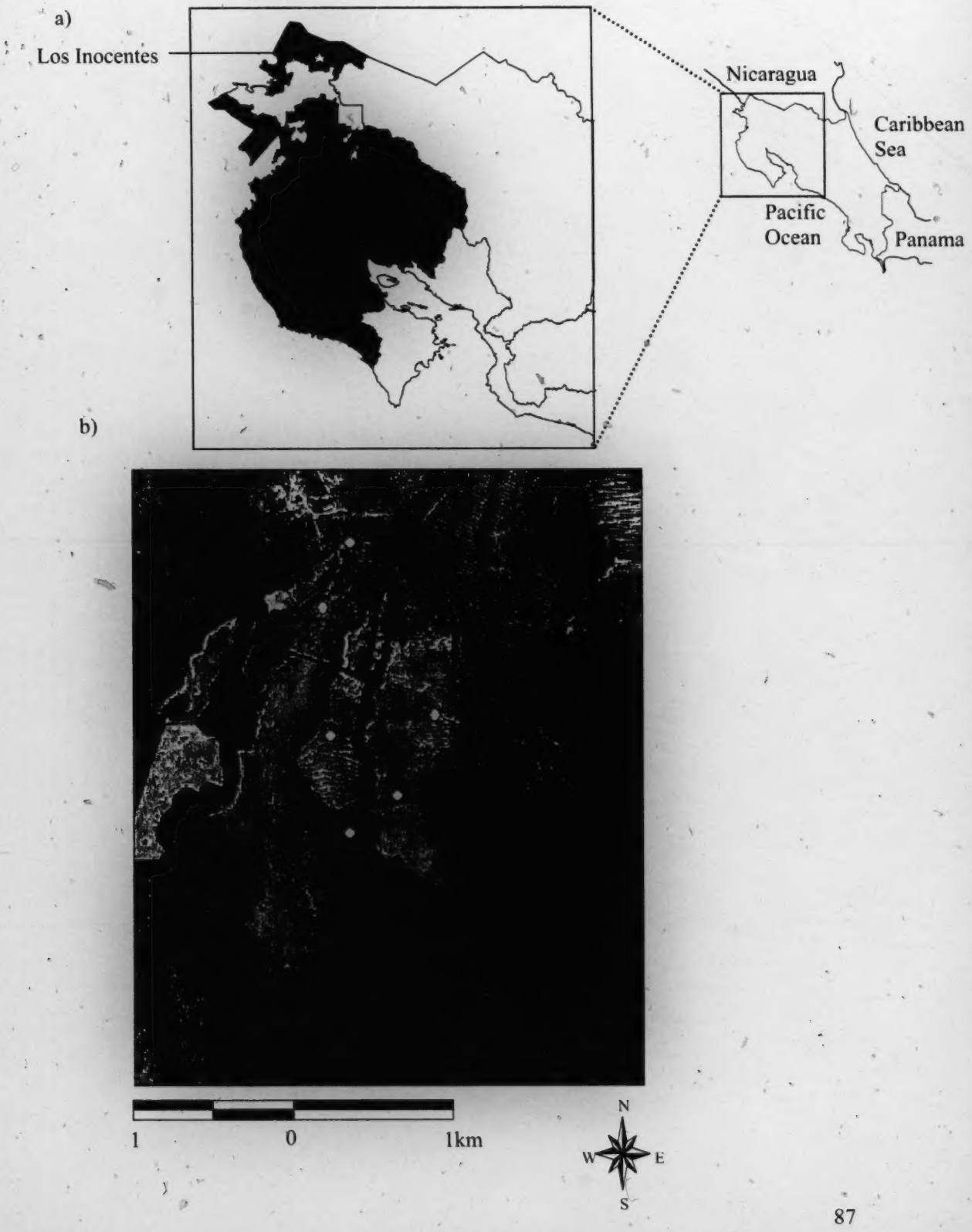

a)
Los Inocentes
Nicaragua
Caribbean
Sea
Pacific
Ocean
Panama
b)
1
0
1km
N
W
E
S

Figure 3.1 a) Los Inocentes (star) in the province of Guanacaste (green), Northwestern Costa Rica. Guanacaste Conservation Area (ACG) is depicted in beige (terrestrial) and blue (marine). The ACG represents a large portion of the remnant dry forest in the country. b) Quickbird multispectral image (2m spatial resolution) of the Los Inocentes property. Band 4 is displayed in red, 3 in green and 2 in blue. The circles represent the locations of the twelve sites on the Los Inocentes property. White = pasture, yellow = early, green = intermediate, blue = late.

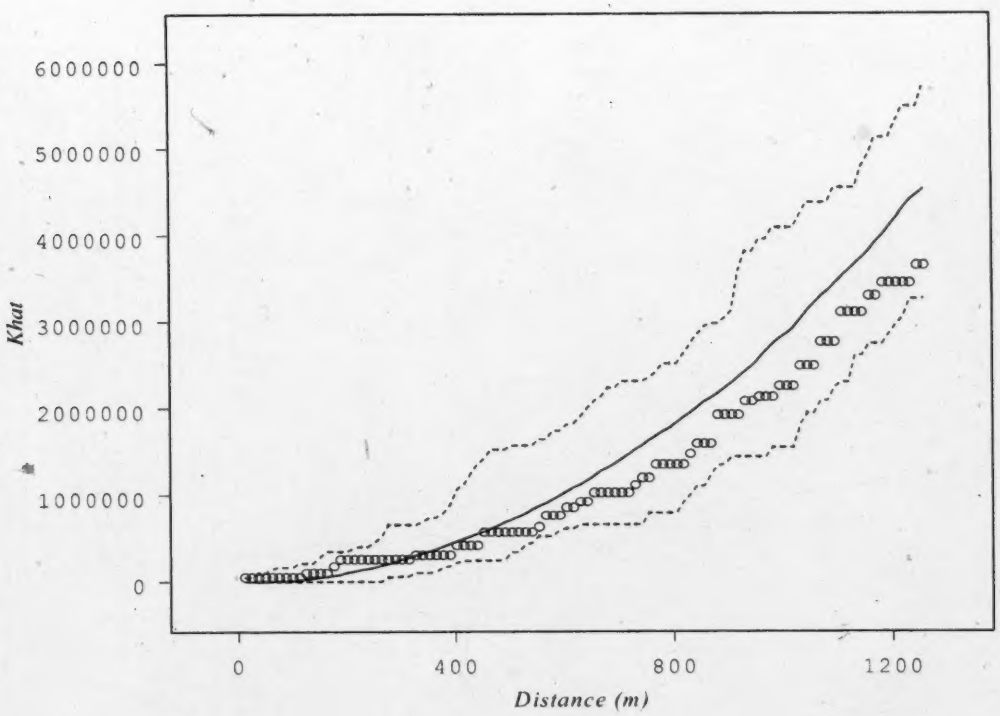



Figure 3.2. Ripley's K function for a spatial point pattern. Solid line indicates the mean for a random distribution, dashed lines indicate the 95% confidence intervals. Open circles represent each of the 100 scales simulated.

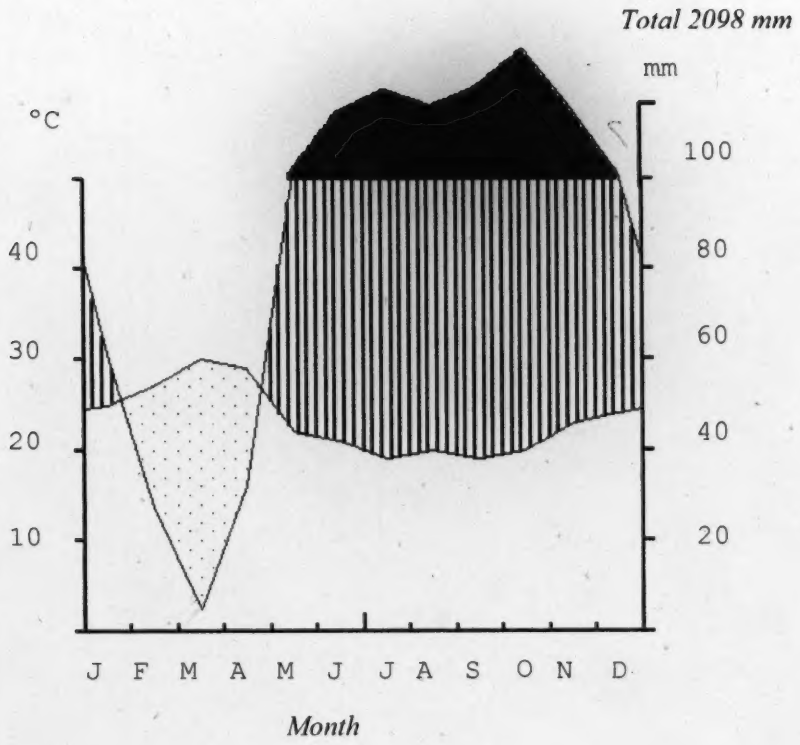



Figure 3.3: Climate diagram for Los Inocentes, Costa Rica. The mean monthly temperature (°C) and the monthly precipitation (mm) are scaled to represent the potential evapotranspiration. Dry months are represented by the dotted areas, humid months by the vertical lines and months with rain in excess of 100mm are in solid black. Diagram created with ECD, Haase 2000.

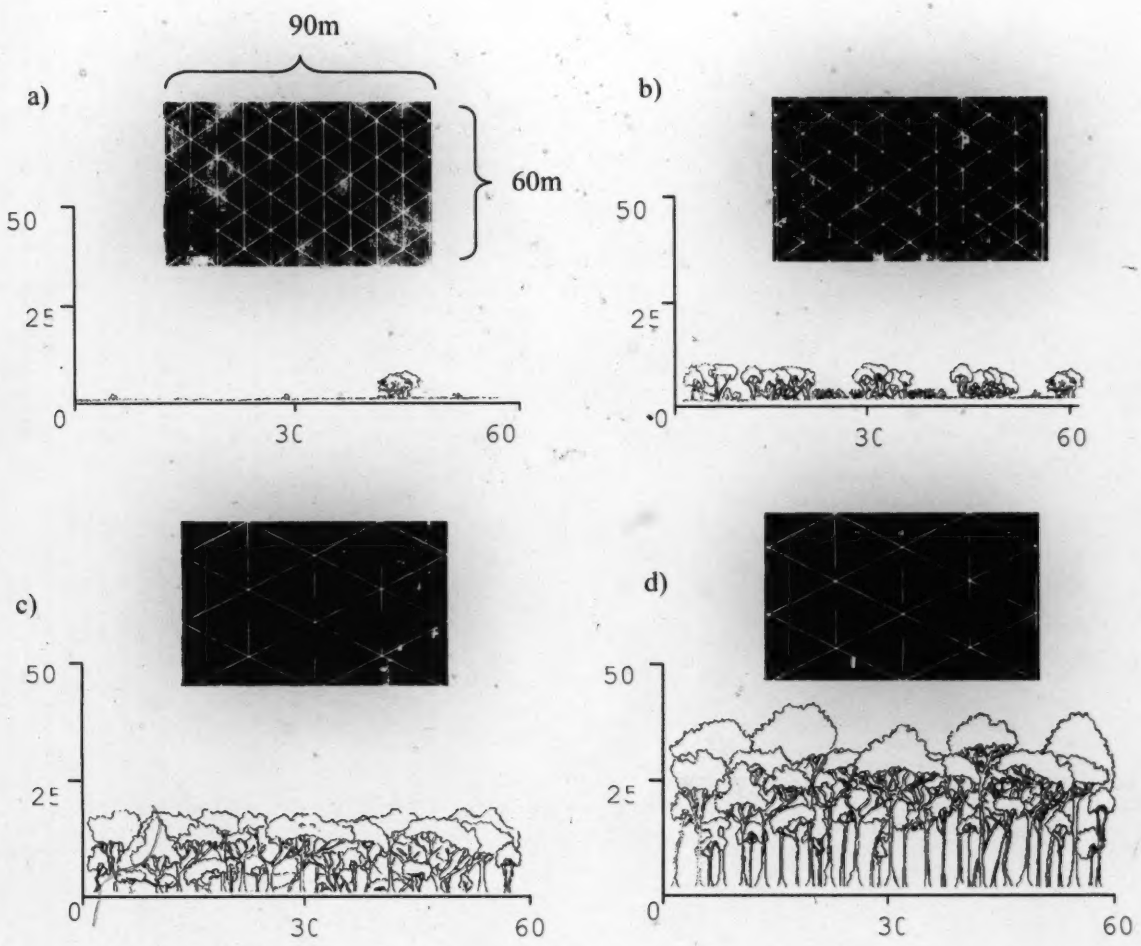



Figure 3.4. Idealized profiles of the four successional stages a) very early, b) early, c) intermediate and d) late adapted from Holdridge et al. 1971 with permission from author. Inset: Quickbird panchromatic band (0.6m spatial resolution) image of an example of each successional stage with LAI sampling scheme superimposed. LAI measurements were taken at the apex of each triangle in the direction of the long axis.

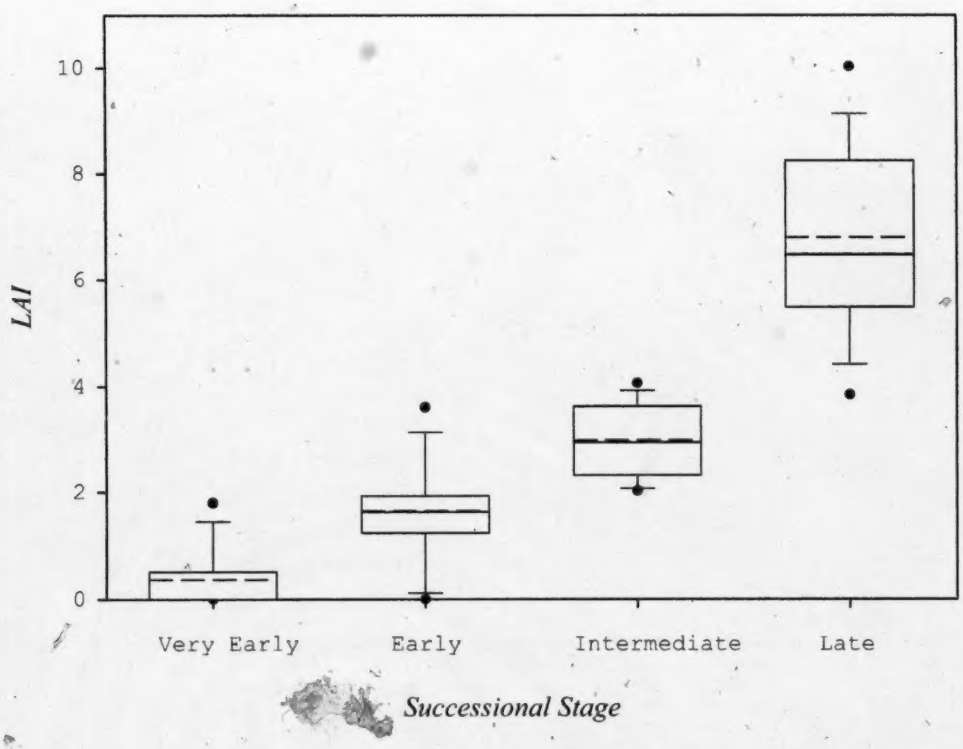
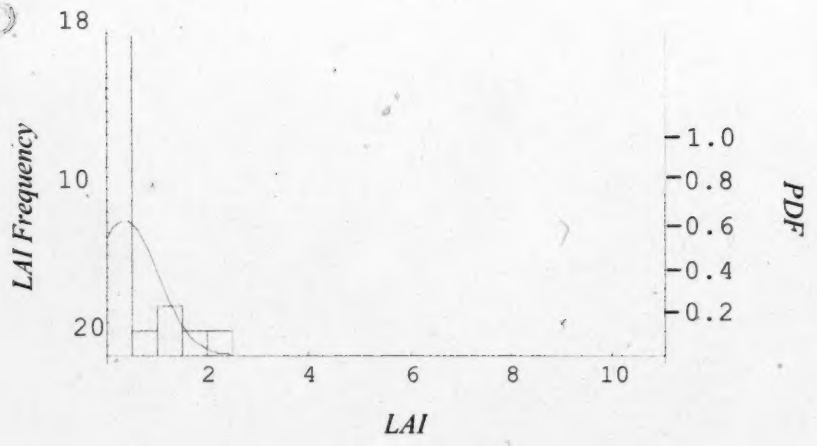
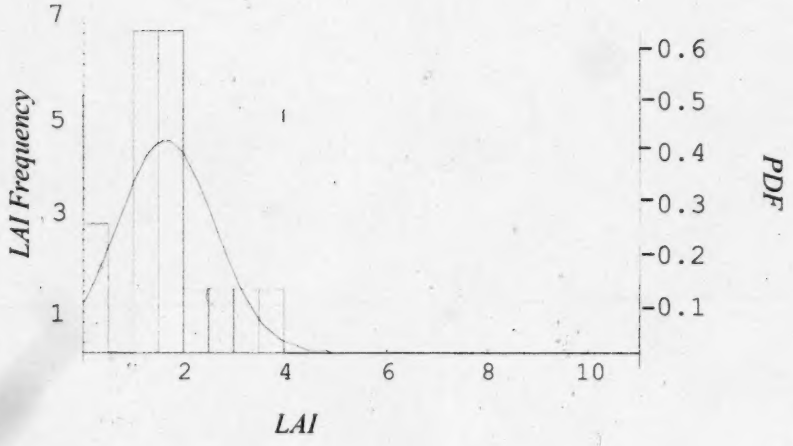



Figure 3.5: Leaf area index of each successional stage. The boundaries of the boxes indicate the 25th and 75th percentiles. The whiskers above and below the boxs indicate the 90th and 10th percentiles and the dots the 5th and 95th percentile outliers. The mean is indicated by a solid line and the mean by the dashed line.

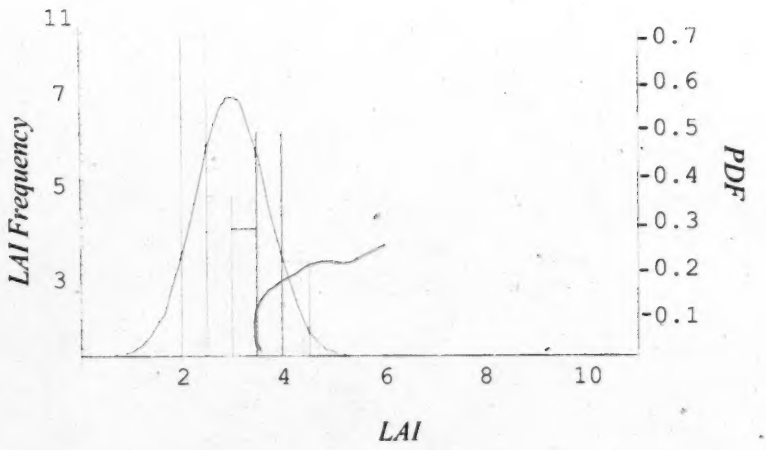
a)


18
10
20
LAI Frequency
1.0
0.8
0.6
0.4
0.2
PDF
2
4
6
8
10
LAI

b)


7
5
3
1
LAI Frequency
0.6
0.5
0.4
0.3
0.2
0.1
PDF
2
4
6
8
10
LAI

c)




d)

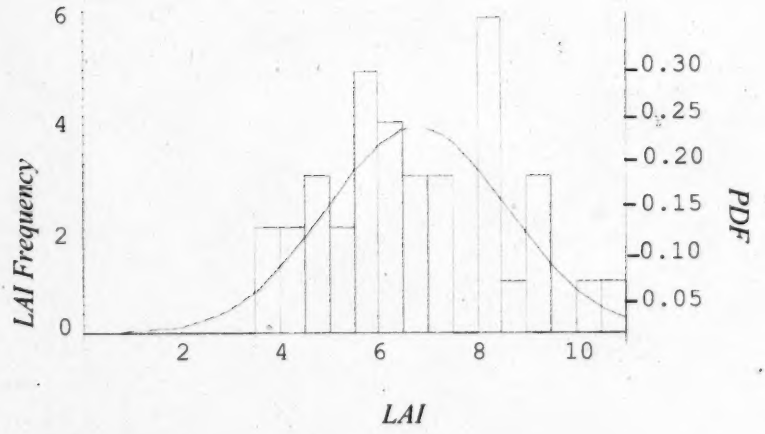
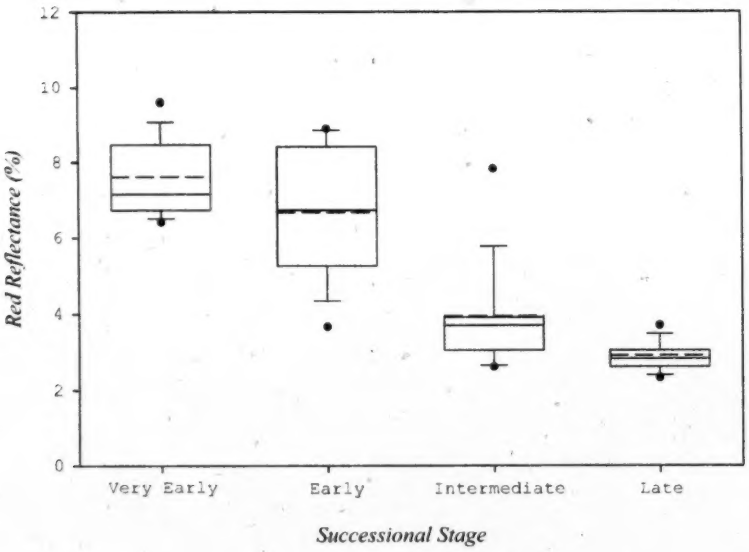



Figure 3.6. Frequency distribution and probability density function (solid line) of LAI in the different successional stages a) very early b) early c) intermediate and d) late.

a)




b)

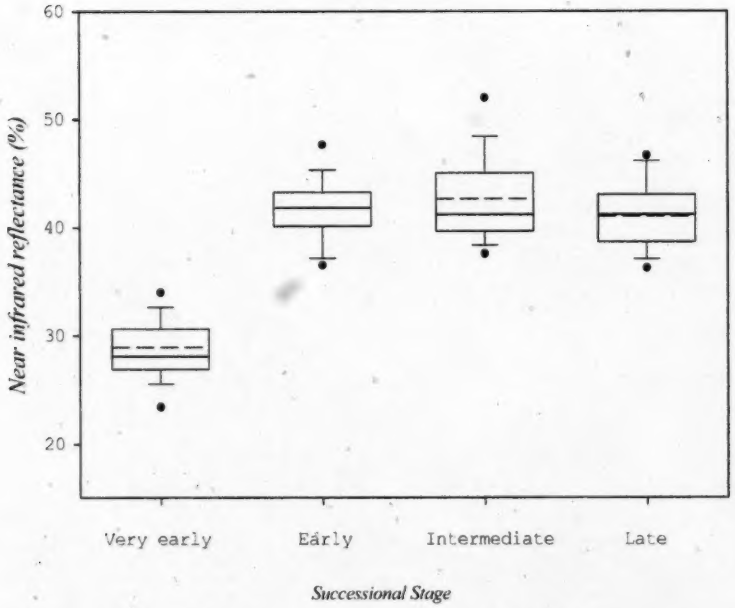
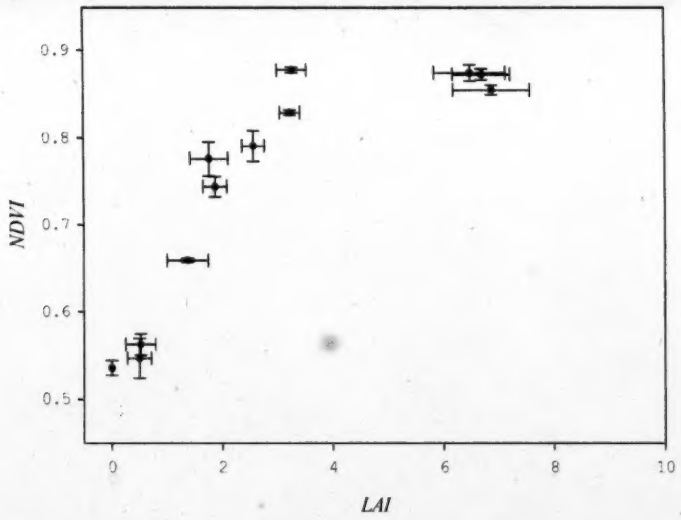
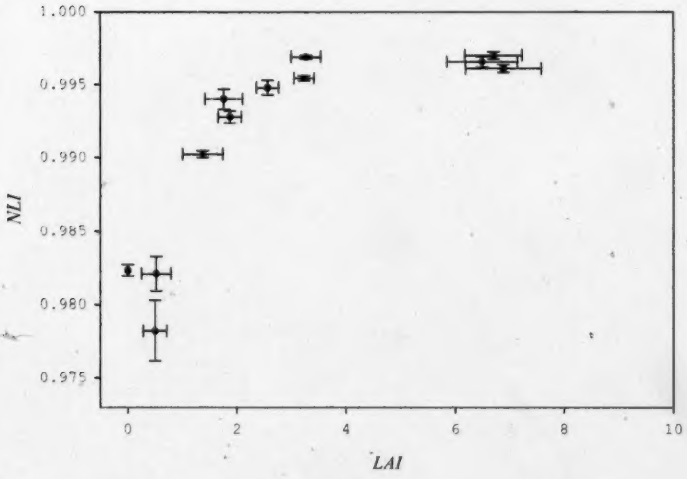



Figure 3.7. a) Red reflectance (%) per successional stage and b) NIR reflectance (%) per successional stage . The boundaries of the boxes indicate the 25$^{th}$ and 75$^{th}$ percentiles. The whiskers above and below the boxs indicate the 90th and 10th percentiles and the dots the 5$^{th}$ and 95$^{th}$ percentile outliers. The mean is indicated by a solid line and the mean by the dashed line.

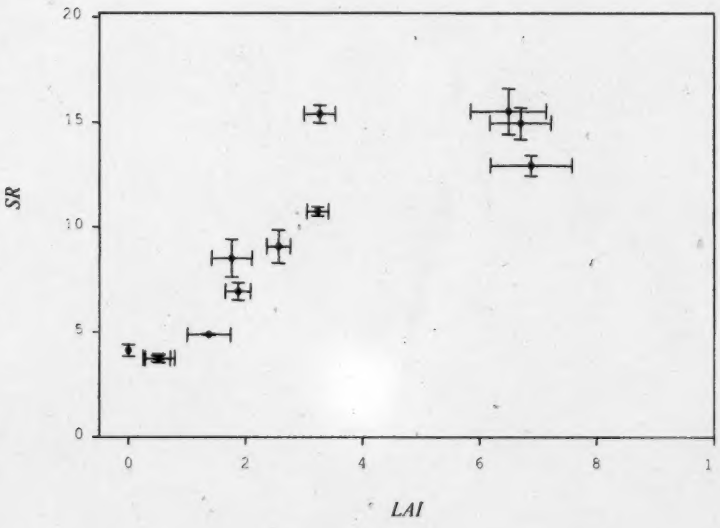
a)


NDVI
0.9
0.8
0.7
0.6
0.5
0
2
4
6
8
10
LAI

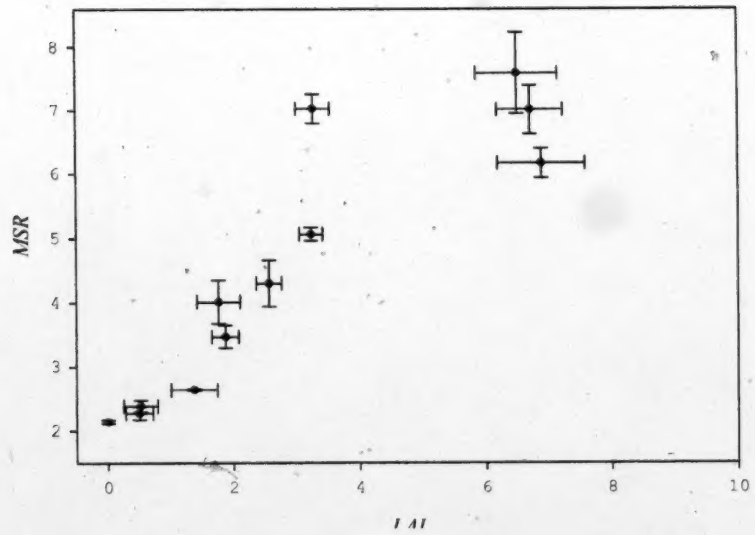
b)


NLI
1.000
0.995
0.990
0.985
0.980
0.975
0
2
4
6
8
10
LAI

c)


SR
20
15
10
5
0
0
2
4
6
8
LAI

d)




e)

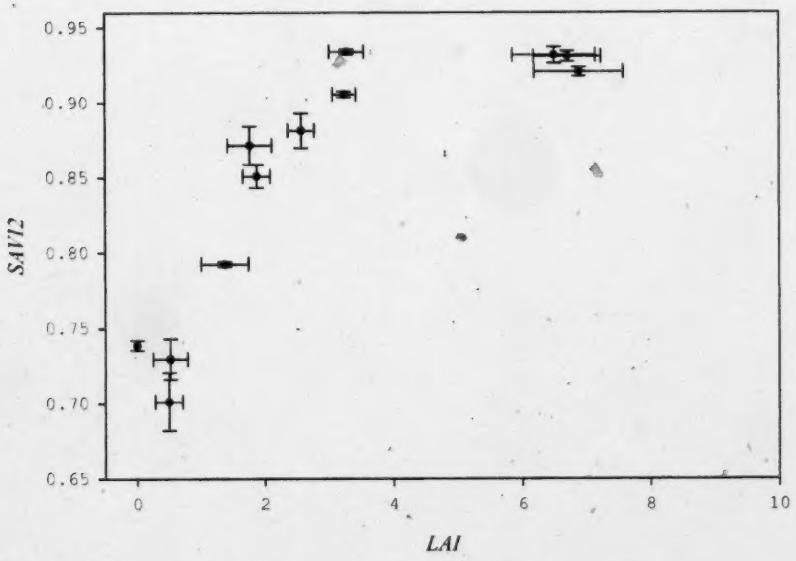
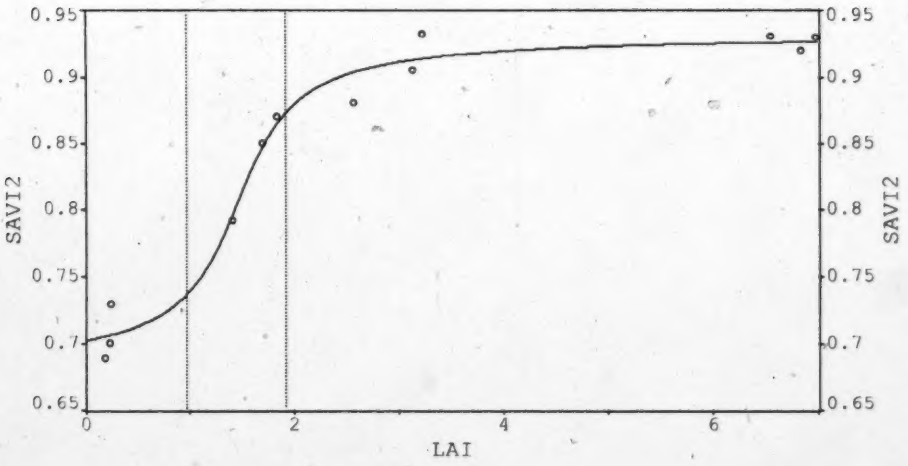
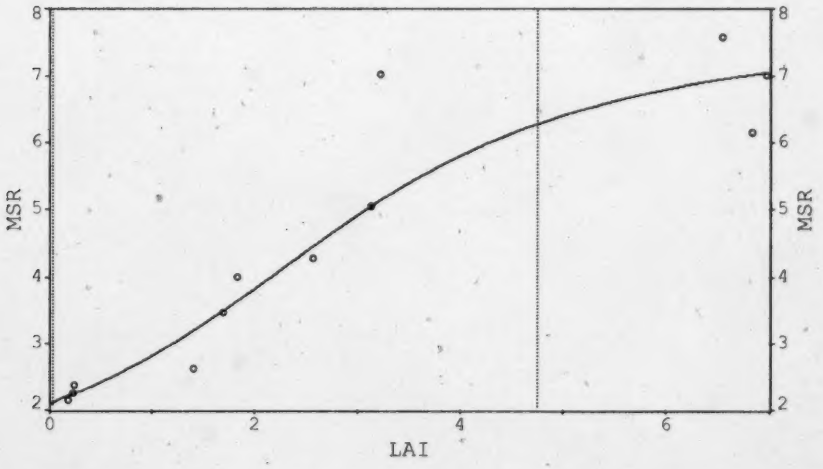



Figure 3.7. LAI vs. the four vegetation indices a) NDVI, b) NLI, c) SR, d) MSR, e) SAVI2. Error bars represent one standard error.

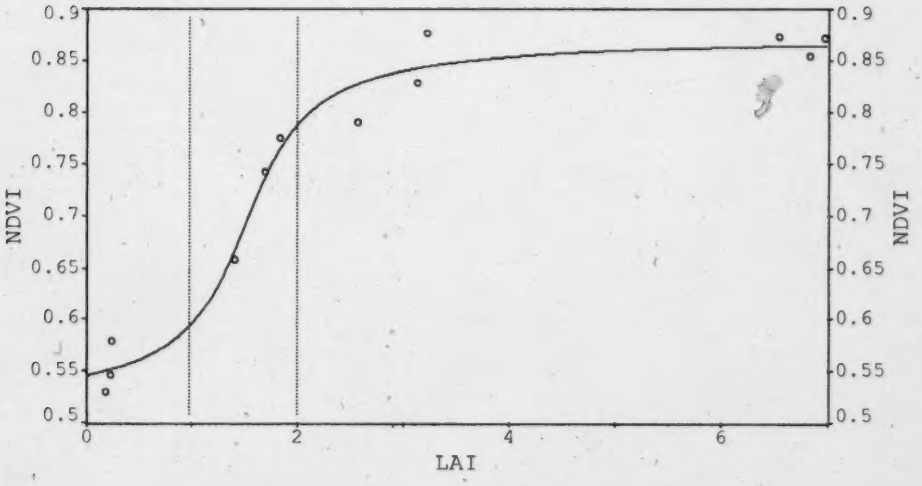
a)


SAVI2
LAI
0.95
0.9
0.85
0.8
0.75
0.7
0.65
0
2
4
6

b)


MSR
LAI
8
7
6
5
4
3
2
0
2
4
6

c)


NDVI
LAI
0.9
0.85
0.8
0.75
0.7
0.65
0.6
0.55
0.5
0
2
4
6

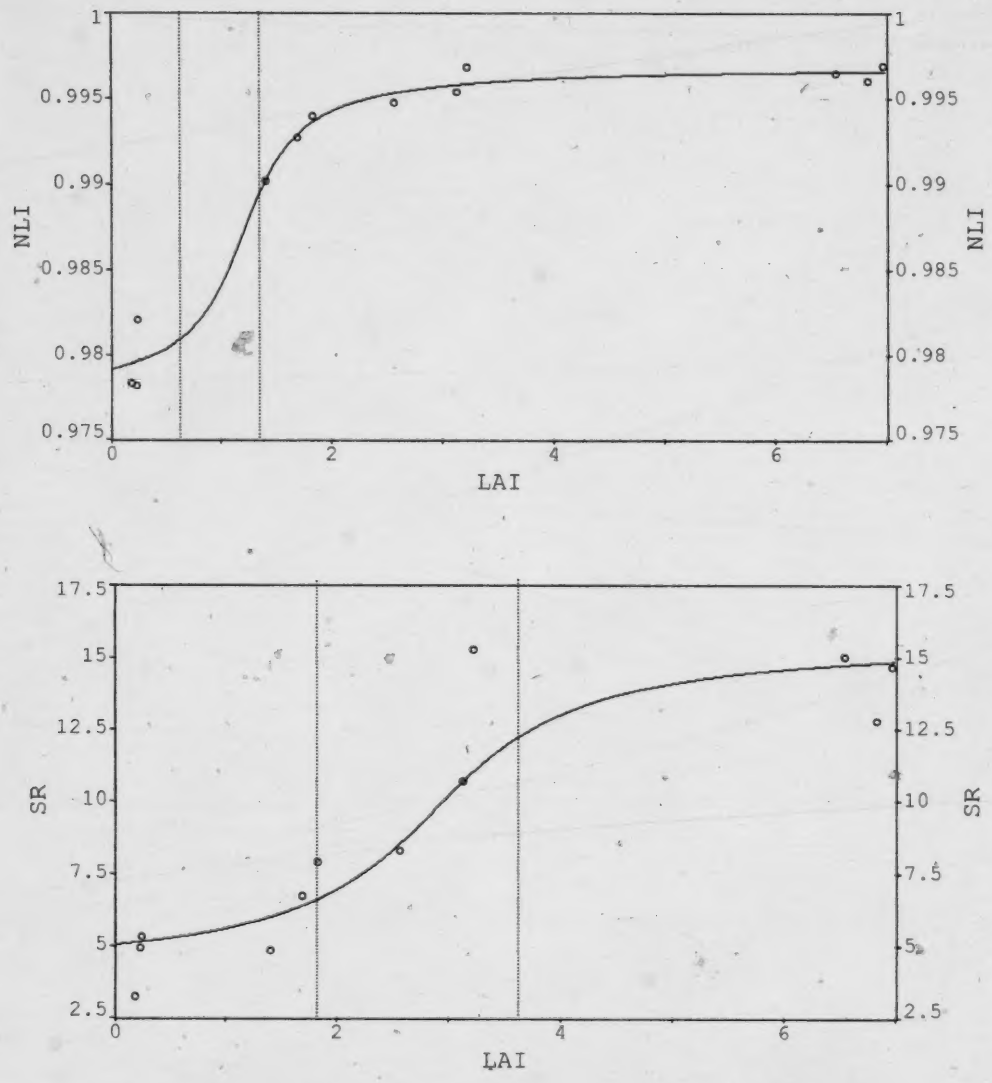
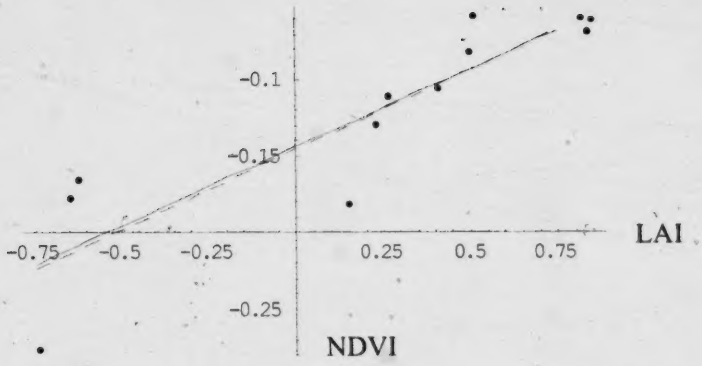
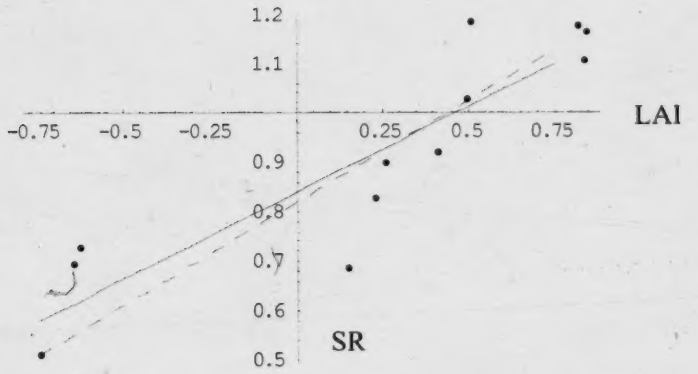



Figure 3. 9. Best-Fit non-linear function: Lorentzian Cumulative function for each SVI. a) SAVI2, b) MSR, c) NDVI, d) NLI, e) SR. Dashed lines indicate upper and lower boundaries of the transition width. Circles represent the mean LAI and mean SVI values for each site.

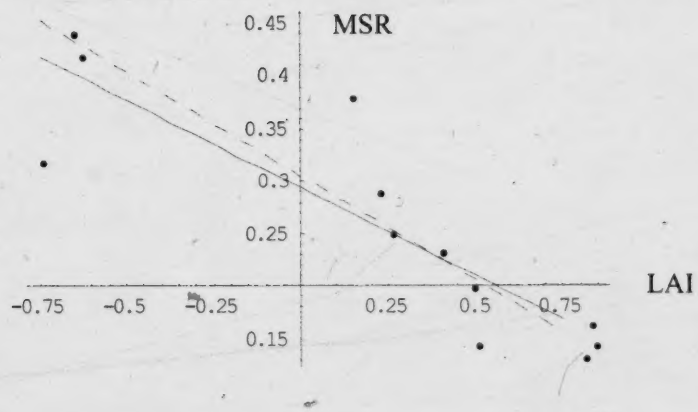
a)


-0.1
-0.15
-0.75
-0.5
-0.25
0.25
0.5
0.75
LAI
-0.25
NDVI

b)


1.2
1.1
-0.75
-0.5
-0.25
0.25
0.5
0.75
LAI
0.9
0.8
0.7
0.6
SR
0.5

c)


0.45
MSR
0.4
0.35
0.3
0.25
-0.75
-0.5
-0.25
0.25
0.5
0.75
LAI
0.15

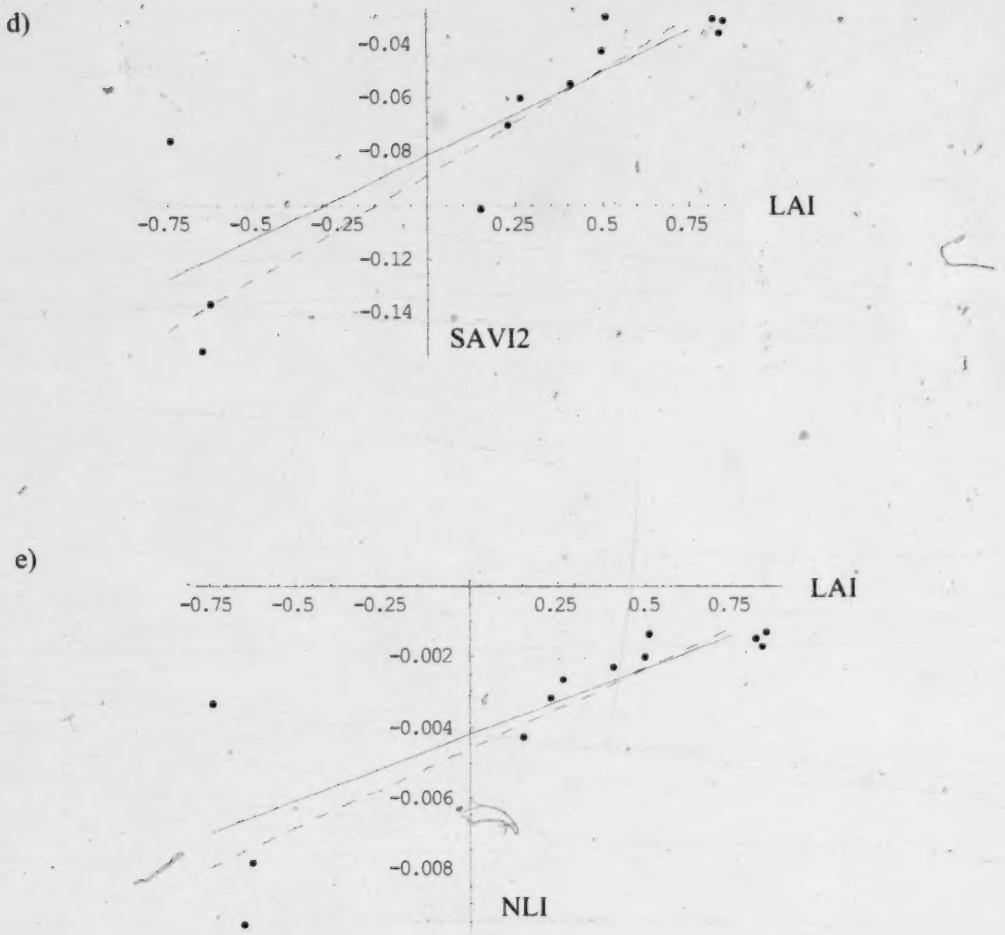



Figure 3.10. Comparison of least squares (solid line) and Theil-Sen linear regression (dashed line) for LAI vs. each SVI. All variables have been log transformed with the exception of MSR which was reciprocally transformed. a)NDVI, b) SR, c) MSR, d) SAVI2, e) NLI

## 4.1. Introduction

The tropical dry forest (*T-df*) encompasses 42% of all tropical forests regardless of climatic affinity (Murphy and Lugo 1986) and contains a wealth of unique biodiversity (Janzen 1988). Yet, it is one of the most fragile and least protected ecosystems (Mooney et al. 1995). In addition, due to anthropogenic, economic and political pressures, this ecosystem has become more degraded than the wet forests. In Mesoamerica (Mexico to Panama) for example, only a small part of the original 500,000km$^2$ extent (Janzen 1988) remains intact (Murphy and Lugo 1995, Ewel 1999).

The *T-df* is characterized by a biotemperature greater than 17ºC and 500 - 2000 mm of precipitation a year (Holdridge 1967) with several months of little or no precipitation (Janzen 1983, Luttge 1997). While containing less species than wet forests (areas with more than 4000mm of precipitation per year), *T-df*s have more structural and physiological diversity in life forms (Mooney et al. 1995). In general, due in part to the long dry season most of the woody species practice drought deciduousness, where they loose their leaves in the dry season as the general leaf phenological response (Gentry 1995, Holbrook et al. 1995). However, the number of species with this response varies with successional stage (stage of regeneration) and topography. A mix of deciduous (with variable timing of leaf fall) and evergreen species gives the *T-df* a phenological complexity not seen in wet forests (Burnham 1997).

A distinguishing characteristic of *T-dfs* is that they defy the well-established trend (Gentry 1988) of increasing species richness as one approaches the equator (Fischer 1959, Chazdon and Denslow 2002): the most diverse Neotropical *T-dfs* are the farthest from the equator in Mexico and South America (Argentina, Brazil, Bolivia and Paraguay)

(Gentry 1995). A second characteristic of *T-df*s is that the most species rich areas are also the driest. Factors affecting species richness include forest fragment size, proximity to seed sources, frequency and type of anthropogenic events (Janzen 1986, Maass 1995). A third important characteristic of *T-df*s is high floristic endemism. Rzedowski (1991) estimates endemism to be as high as 43% in Mexico while Gentry (1982) estimates that regional endemism in South American *T-df*s is as high as 73%, a figure exceeded only by Amazonia. Joly (1970) has estimated that the Cerrado region of the Brazilian dry forest contains up to 70% of all species of certain families as endemics. For example, 91% of the 59 species of Velloziaceae are endemic to the *T-df* in Brazil (Giulietti and Pirani 1988).

Despite these unique characteristics, many studies (ex. Gentry 1982, Hartshorn 1983) have been broad investigations regarding the differences or similarities between *T-df*s and wet forests (Gentry 1995). Others have focused on the effects of water stress (Medina 1995), biomass estimation (Murphy and Lugo 1986, Kauffman et al. 2002) or detailed floristic inventories (Janzen and Liesner 1980, Lott 1985, Martinez-Yrizar and Sarukhan 1990, Gentry 1995, Gonzalez-Iturbe et al. 2002, among others). Many of these detailed studies in *T-df*s evaluate floristic composition without stratification by stages of growth (ex. Holdridge et al. 1971, Gentry 1995, Burnham 1997, Balvanera et al. 2002, Segura et al. 2002, Gillespie et al. 2000, Quigley and Platt 2003) with few exceptions (ex. Lugo et al. 1978, Gonzalez-Iturbe et al. 2002). The *T-df* forest in many areas is not a pristine primary forest, but rather a mosaic of successional stages due to extensive anthropogenic disturbance (Janzen 1986, Arroyo-Mora 2002).

One of the most important and dynamic components of this ecosystem is foliage. It is the element of the forest structure that adapts the most to small temporal changes in the environment (ex. response to water stress or changes in illumination conditions) (Welles 1990). A simple measure of the amount of foliage is the leaf area index (LAI). Leaf area is important because it provides the exchange surface between the photosynthetically active component of the vegetation and the atmosphere (Turner et al. 1999, Fournier et al. 2003, Cohen et al. 2003, Fernandes et al. 2003). Thus, through exchange and regulation foliage controls the light, thermal and hydric conditions within the canopy (Fournier et al. 2003).

In this study our objective is to 1) describe the floristic composition, species diversity and similarity between three stages of secondary *T-df* regeneration through the use of ecological indices, 2) investigate the influence of the previous land use history on the species composition and 3) describe the changes in LAI as a function of the season and the successional stage in a tropical dry forest in NW Costa Rica. Because earlier studies have often treated the forest as an entity without segregation into successional stages and our study area is a secondary forest, the emphasis here is on evaluating structural characteristics, species composition and LAI across different successional stages in an attempt to describe and control for the variability in physiognomy and LAI inherent in a regenerating forest.

## 4.2. Methods

### *4.2.1 Study Area*

A large area of Costa Rica's *T-df* (according to the Holdridge Life Zone Classification System) is in the Guanacaste Conservation Area, which originated as an

extension to the Santa Rosa National Park (Figure 4.1) (10° 48' 53" N, 85° 36' 54" W) in the Province of Guanacaste. The Santa Rosa National Park is composed of a mosaic of pasture and secondary growth in various stages of regeneration with areas that have different land use histories, past land use intensities as well as different occurrences of discrete anthropogenic events such as fire. The climate diagram (Walter 1971) for the park is shown in Figure 4.2. It illustrates the seasonality of the precipitation and the length of the dry season. In addition, the total yearly precipitation in the park is highly variable (915 - 2558mm per year) (Janzen 1993).

*4.2.2 Site Selection*

The sites for this study were chosen in two steps. The first step made use of the Normalized Difference Vegetation Index (NDVI) (Running et al. 1986, Goward et al. 1991, Chen 1996) calculated from an IKONOS (4 spectral bands, 4m spatial resolution) satellite image acquired in March 2001. NDVI is calculated as follows:

$$NDVI = \frac{\rho_{NIR} - \rho_{Red}}{\rho_{NIR} + \rho_{Red}} \qquad (1)$$

An explanation of all symbols for the various formulae in this paper can be found in Appendix I. This index (NDVI) has been used to relate biophysical variables to remotely sensed data (Turner et al. 1999) and has one of the best-documented relationships to LAI (Chen 1996). Potential sites were identified on the NDVI image as discrete areas covering the full range of NDVI values. Known pastures were excluded from the analysis. The second step consisted of visiting these sites and evaluating the

structure based on the descriptions of three successional stages (early, intermediate, late) identified and described from the same IKONOS image by Arroyo-Mora (2002).

### *4.2.3 Field Measurements*

#### *4.2.3.1 Structure and Composition*

In ten early successional stage plots (20m x 50m – 0.1ha) (Figure 4.3), we identified and measured the Diameter at Breast Height (DBH) of all living woody stems with a DBH greater than 5cm. We also measured the height of the six tallest trees in each plot (twice the number of trees recommended by Holdridge (1967)). These same measurements were repeated in ten intermediate and six late successional plots of the same dimensions. The descriptions of the successional stages (early, intermediate and late) were adapted from Arroyo-Mora (2002).

#### *4.2.3.2 Leaf Area Index*

We used the LAI-2000 Plant Canopy Analyzer (PCA) to estimate LAI in 16 of the 26 structural plots. The area for the LAI measurements was 30m x 60m (Figure 4.3). The PCA is an optical instrument designed to derive the amount of radiation that penetrates the canopy. It is composed of five concentric silicon rings with fields of view centered on 7°, 23°, 38°, 53° and 68° and receives diffuse sky radiation (<490nm to minimize scattering effects) through a hemispherical lens (Welles and Cohen 1996, Planchais and Pontailler 1999). We took reference (above canopy radiation) measurements both before and after each site. In addition, the sensor was fitted with a 45° view cap to eliminate the image of the operator from the field of view. Values of effective LAI (LAIe) were calculated from the PCA using the readings from the first four rings (field of view less

than 68°). We assumed that the foliage was randomly oriented and therefore, refer to the LAIe estimations as LAI values.

As radiation passes through the canopy, there is a chance it will be intercepted by canopy elements (branches, leaves, etc.). This probability of interception is proportional to the path length, the density of the canopy elements and the foliage orientation (Welles and Norman 1991). A ray of sunlight passing through the canopy from a zenith angle θ and an azimuth angle Φ has the probability of not being intercepted by the canopy of T(θ,Φ)(Welles and Norman 1991):

$$T(\theta, \Phi) = \exp[-G(\theta, \Phi)\,\mu\, S(\theta, \Phi)] \tag{2}$$

where

$$G(\theta)\,\mu = -\frac{\ln(T(\theta))}{S(\theta)} \equiv K(\theta) \tag{3}$$

and

$$\mu = 2\int_0^{\frac{\pi}{2}} \frac{-\ln(T(\theta))}{S(\theta)} \sin\theta\, d\theta \tag{4}$$

For a homogeneous canopy Welles and Norman (1991) solve for LAI (L) by the following equation:

$$L = 2\int_0^{\frac{\pi}{2}} -\ln(T(\theta))\cos\theta\sin\theta\, d\theta \tag{5}$$

True LAI is a measure of foliage. However, trunk, branches etc. intercept incoming light and contribute to the estimation of LAIe (Fournier et al. 2003). In general, optical instrument cannot discriminate between foliar and non-photosynthetic components of the canopy. True foliar LAI ($L_f$) can therefore, be calculated from (Chen et al.1997):

$$L_f = (1-\alpha)\times \frac{\mathrm{LAI}_e}{\Omega} = (1-\alpha)\times \mathrm{LAI}_e \times \frac{\Upsilon_E}{\Omega_E}$$

However, α needs to be estimated destructively where α is the ratio of the wood area index and LAIe (Fournier et al. 2003). The term $\Omega_E$ is also very difficult to assess. One of the most recent proposals for estimating this term is from Chen and Cihlar (1995) and Chen (1996). Their method involves the calculation of gap fraction distribution in an aggregated and random canopy. The term $\gamma_E$ is only a concern for needle-leaf canopies. In this analysis, since we assumed a random orientation of the foliage, we assumed Ω=1 and therefore, used the LAIe values for LAI. We are able to approximate α from the dry season measurements when the majority of the woody vegetation is leafless.

We measured 16 LAI plots in total (7 early, 6 intermediate and 3 late). Based on The random spatial distribution at all scales for all 26 sites was tested using Ripley's K function (Ripley 1976) (Chapter 3). Ripley's K function can summarize a point pattern or test a hypothesis about a spatial point pattern. It describes characteristics of the point processes at many distance scales (Freeman and Ford 2002). In many cases, data can have a combination of spatial patterns based on the scale (ex. clustered at small scales and random at large scales) (Diggle 1983). With Ripley's K function, these combinations can be seen. Our results indicate that all sites have a random spatial distribution at all scales between 0 and 5000m (Figure 4.4).

The LAI measurements were made using an offset-grid sampling scheme designed for the LAI2000 in *T-df* environments where the maximum surface area of the plots was covered without overlap of the measurements (Figure 4.3). Because the area

sampled by the PCA is largely dependent on the height of the canopy (LI-COR 1992), the spacing between measurements varied between successional stages.

In each early plot we took 100 measurements, each covering a roughly triangular area of 5 x 6m (Figure 4.3a) covering 83% of the total plot area. In each intermediate plot we took 36 measurements, each covering roughly a triangular area of 8 x 10m (Figure 4.3b) covering 80% of the total plot area. And in each late plot we took 12 measurements, each covering an area of 15 x 18m (Figure 4.3c) encompassing 90% of the total plot area. In addition, the effect of instrumental variation on the variability of LAI calculations was assessed using 1 to 10 estimates of the same measurement. There was no significant variation (coefficient of variation = 0.005) in the estimate of LAI of the same triangular area from 1 to 10 measurements. Therefore, each measurement per plot was taken in triplicate the average of which was used in the LAI calculations. For this study, LAI was measured nine times from December 2001 to April 2003 (Table 4.1).

In addition, we placed 30 standard 0.5m x 0.5m mesh leaf litter traps in three plots (one of each successional stage) for a total of 90 traps. In each plot, the traps were located in ten offset rows of three in order to cover as much area as possible. Litter was collected five times during the 2002-2003 leaf fall cycle at one-month intervals. The material was sorted per species and oven dried at 80° C to constant weight (2.5 hours). Specimens that were not identifiable to species were classified into pseudo-species. A third class, "unidentifiable", contains all the remains that are beyond identification to even pseudo-species.

*4.2.4. Diversity, Similarity and Complexity*

Floristic composition, diversity and similarity were measured with quantitative and qualitative indices. To estimate diversity we calculated the Brillouin Index (HB) (Magurran 1988) and the Shannon Diversity index (H`) (Magurran, 1988) and their respective measures of evenness for each stage. The Brillouin Index (HB) is defined as:

$$HB = \frac{\ln N! - \sum \ln n_i!}{N} \tag{7}$$

Evenness for HB was calculated by the following formulae (Magurran, 1988):

$$E = \frac{HB}{HB_{max}} \tag{8}$$

where:

$$HB_{max} = \frac{1}{N} \ln \left( \frac{N!}{\left( \left[ \frac{N}{S_p} \right] ! \right)^{S_p - \left( N - S_p \left[ \frac{N}{S_p} \right] \right)} \times \left( \left[ \frac{N}{S_p} \right] + 1 \right) ! ^{N - S_p \left[ \frac{N}{S_p} \right]}} \right) \tag{9}$$

The Shannon Diversity index (H`) is defined as:

$$H' = -\sum p_i \ln p_i \tag{10}$$

Evenness for H` was calculated as follows (Magurran 1988):

$$E = \frac{H'}{\ln S_p} \tag{11}$$

To evaluate β diversity (variation in species composition within landscapes) we assessed the similarity in species composition between the different stages (landscapes). We used two indices (one qualitative and one quantitative). The first index, the Sørenson coefficient is a qualitative measure of similarity ($C_s$) (Magurran, 1988):

$$C_s = \frac{2j}{(a+b)} \tag{12}$$

For a quantitative measure of β diversity between stages we used a modified version of the Morista-Horn index ($C_{MH}$) (Magurran 1988):

$$C_{MH} = \frac{2\sum(an_i \times bn_i)}{\left(\frac{\Sigma an_i}{aN^2} + \frac{\Sigma bn_i}{bN^2}\right) \times aN \times bN} \tag{13}$$

In order to examine the floristic similarity between sample plots of all successional stages, we calculated a Jaccard's similarity coefficient (qualitative) ($C_j$) defined as (Magurran 1988):

$$C_j = \frac{j}{a+b-j} \tag{14}$$

Subsequently, we performed an agglomerative hierarchical cluster analysis using the agnes-algorithm applied to a matrix of Jaccard similarity coefficients between the plots of all stages. The algorithm begins the clustering by assigning each observation to a cluster which it subsequently merges until one large cluster is formed, containing all the observations (Struyf et al 1997). For each stage the two "nearest" clusters are combined to form a larger cluster at a higher level. We used the "average" method with the Euclidean distance metric option where the distance between two clusters is the average of the dissimilarities between the points of the two clusters (Struyf et al 1997).

As a measure of ecosystem complexity we computed the Holdridge Complexity Index ($C_{HCI}$) (Holdridge 1967):

$$C_{HCI} = \frac{H \times D \times S_p \times G}{1000} \quad (15)$$

where:

$$G_b = \frac{\pi}{40000} + \frac{\sum \zeta^2}{A} \quad (16)$$

Lugo et al. (1978) modified $C_{HCI}$ for secondary forests. While the index and procedures are the same as the original $C_{HCI}$, all the trees with DBH greater than 5cm are measured (instead of all trees with DBH exceeding10cm). For this study, we adopted the modified $C_{HCI}$.

*4.2.5 Structure*

We performed a Fuzzy partitioning analysis of structural variables (H, Gb, Sp) for all plots with the fanny algorithm (into three clusters). Fuzzy partitioning is different from crisp clustering methods (where each observation is assigned to only one cluster) because it assigns fractal membership (partial membership) of each observation to multiple clusters (in this case into all three clusters).

*4.2.6 Statistical Analysis*

In order to choose between classical statistical tests (ex. ANOVA) and non-parametric statistics (ex. Kruskal-Wallis) we tested all data sets with the D'Agostino-Pearson Test for Departure from Normality (Abbell et al. 1998). If the data did not meet the assumptions of normality we used non-parametric tests.

## 4.3. Results

### *4.3.1 Species Composition*

The species composition for each successional stage is illustrated in Table 4.2. We identified a total of 3015 individuals representing 159 woody species (55 families). In total, there were 33 families in the early stage represented by 1125 individuals. Four of these families individually compose greater than 5% of the total individuals from this stage (Table 4.3). Cochlospermaceae, Sterculiaceae, Fabaceae and Verbenaceae. In the intermediate stage, we identified a total 1137 individuals belonging to 45 families. Six families individually compose greater than 5% of the total individuals in this stage (Table 4.3). Boraginaceae, Cochlospermaceae, Euphorbiaceae, Fabaceae, Rubiaceae and Tiliaceae. From a total of 45 families and 751 individuals in the late stage there are six families (Table 4.3) that individually constitute greater than 5% of the total individuals; Burseraceae, Euphorbiaceae, Fabaceae, Hippocrateaceae, Rubiaceae and Sapindaceae.

### *4.3.2 Measures of Diversity*

Table 4.4 illustrates the Brillouin and Shannon Diversity indices along with their respective measures of evenness. The Brillouin index indicates that the highest species diversity is found in the intermediate stage (HB = 3.91), followed by the late (HB=3.68) and early (H=2.56) stages. Since this index does not attempt to extrapolate to the entire population, all the values are statistically significant (Magurran 1988). According to the Shannon Diversity Index, the intermediate stage has the most species diversity (H`=4.08). In addition, similar to the Brillouin Index, it indicates that the late stage (H`=3.88) is

more diverse than the early stage (H`=2.66). The Shannon diversity index found significant differences (t Test) between stages (early – intermediate $t = 6.79$, $P < 0.001$; intermediate – late $t = -3.97$, $P < 0.001$; early – late $t = 5.20$ $P < 0.001$). The evenness values for the Brillouin index are lowest for the early stage (E=0.424), followed by the intermediate (E=0.647) and then the late stage (E=0.653). A similar pattern is observed for the Shannon index.

*4.3.3 Measures of Similarity*

The Morista-Horn and Sørenson similarity coefficients are shown in Table 4.5. According to Sorenson's index (qualitative), the greatest similarity is between the intermediate and late stages (64%). The index also found a 55% similarity between the early and intermediate stages and a 46% similarity between the early and late stages. The Morista-Horn index (quantitative) found the greatest similarity between the intermediate and late stages where it found a probability of 0.52 to find an individual of the same species in a sample event of the two stages. The index dropped to 0.30 between the early and intermediate stages and dropped even further to 0.26 between the early and late stages.

Figure 4.5 illustrates the similarity in species composition for all plots from an agglomerative- hierarchical cluster analysis. The analysis was performed on a matrix of Jaccard similarity coefficients. In total there are 25 levels of height (the vector with the distances between merging clusters) ranging from 0.89 to 2.12.

*4.3.4 Structure*

A summary of the structural data is shown in Table 4.6. Since the structural data are normally distributed (Pearson Correlation Coefficient $P > 0.05$), all values in the table are mean values. Significant differences were found for all variables with the exception of density using a One-Way ANOVA (height: F=26.8, P<0.001; basal area: F=35.6, P<0.001; number of species: F=18.2, P<0.001; Holdridge Complexity Index: F=34.7, P<0.001). With pair-wise Welch Modified Two-Sample t-Tests (variance not assumed equal), the mean height of the early stage was found to be different than the intermediate and late stages (t = -2.25, P=0.04 and t = -6.43, P<0.001). The height of the intermediate stage was also found to be different than the late (t = -3.65, P<0.001). The basal area of the early stage is significantly different than the intermediate and late stages (t = -3.52, P<0.001 and t = -5.84, P<0.001). The basal area of the intermediate stage was also found to be different than that of the late stage (t = -2.32, P = 0.04). The median number of species was different in the early stage than in the intermediate and late stages (t = -5.48, P<0.001 and t = -3.82, P < 0.001). The number of species in the intermediate stage was not different than in the late stage. The Holdridge Complexity Index is significantly different in the early stage than in either the intermediate or late stages (t = -2.60, P=0.02 and t = -5.01, P<0.00). The $C_{HCI}$ is also different in the intermediate stage than in the late stage (t = -3.63, P=0.01).

Figure 4.6 illustrates the cluster diagram of a fuzzy partitioning analysis (into three clusters) with (Euclidean distance metric) performed on the structural data with the fanny algorithm in S+. The results of the closest hard clustering (where the highest

fractal membership from the fuzzy partitioning indicates the membership class) indicate that of the ten early sites nine were assigned to a single cluster (one site – a more developed early site - was assigned to the cluster with the intermediate sites). Of the ten intermediate sites six were assigned to one cluster (four were assigned – more developed intermediate sites - to the cluster with the late plots). And of the six late plots, all six were assigned to one cluster.

*4.3.5 Leaf Area Index*

Leaf Area Index values for the three stages during the two extreme seasons (dry and wet) are illustrated by the box plots in Figure 4.7. The values for the minimum and maximum LAI values are listed in Table 4.7. Because the LAI data are not normally distributed (D'Agostino-Pearson Test for Departure from Normality), we used non-parametric statistics in this analysis. Kruskal-Wallis tests for dry and wet season LAI values indicate a significant increase in median LAI values through the gradient of the successional stages ($P < 0.001$ in both cases). In the wet season, LAI in the intermediate stage is significantly greater than the early stage ($P<0.001$). In addition, the LAI for the late stage is significantly greater than for the intermediate stage ($P<0.001$). In the dry season, LAI is significantly greater in the intermediate stage than in the early and late stages ($P<0.001$ and $P=0.03$). The LAI values from the late stage are greater than for the early stage ($P<0.001$). There is spatial heterogeneity in LAI for all stages (Figure 4.8) in both seasons due to canopy gaps, variations in the vertical and horizontal planes of the canopy and the presence of a species (*Jaquinia nervosa*) that practices a wet season deciduous leaf phenology.

Seasonal variation in LAI for the three seasons is illustrated in Figures 4.9 a-c. The data were fitted to a fourth order polynomial to illustrate the seasonality of LAI. By solving for $x = 0$ for the derivative of the fourth order polynomial functions, it is possible to find the months where LAI is at it's minimum and maximum. The three stages yielded different results (Figure 4.9d): the minimums for the three stages are the last week of January, last week of March and mid February respectively. Similarly the maximum LAI values were reached during the mid September for the early stage mid November for the intermediate stage and mid October for the late stage.

For the leaf litter we tried to identify as many of the leaves to species as possible in order to construct more precise area-weight allometric curves in the future. However, there is a large number we could only identify to pseudo-species (Figure 4.10a). These pseudo species account for only a small amount of the total weight in each stage (Figure 4.10b). Because of the unidentified remains in the 'unidentifiable' category, the values in Figures 4.10a and 4.10d are the minimum number of species in each stage.

We found that there is a significant difference in total mean leaf fall for the three stages ($F = 4.36$, $P = 0.039$). In addition the pair-wise tests found differences in total mean leaf fall between the early (2.6kg) and intermediate (4.5kg) ($t = -6.38$, $P < 0.001$) and the intermediate and late (3.1kg) ($t = 4.90$, $P < 0.001$) but not between the early and late ($t = -1.81$, $P = 0.076$). As can be seen in Figure 4.10c, the greatest amount of leaves fell in the fourth collection for the early (29%) and late (36%) stages. However, for the intermediate stage, the greatest amount of leaves fell in the last collection (36%) Therefore, the leaf production was greater and the leaves persisted longer in the intermediate stage. As can be seen in Figure 4.10d, the fourth collection had the greatest

number of species in each stage (61, 68 and 47 species respectively). Based on the identified and pseudo-species collected it is the contribution of the lianas to the total leaf weight sets the intermediate stage apart from the other two stages.

## 4.4. Discussion and Conclusions

### *4.4.1 Species Composition*

Many studies in tropical dry forests evaluate floristic composition without stratification by stages of growth (ex. Holdridge et al. 1971, Gentry 1995, Burnham 1997, Balvanera et al. 2002, Segura et al. 2002, Gillespie et al. 2000, Quigley and Platt 2003) with few exceptions (ex. Lugo et al. 1978, Gonzalez-Iturbe et al. 2002). However, the differences in species composition in the different successional stages seen in Tables 4.2 and 4.4 indicate that substantial information would be missed if an area of *T-df* is evaluated as a homogenous entity. Results about species composition would be biased because the species are not equally abundant in all stages. For example, *Cochlospermum vitifolium* and *Guazuma ulmifolia* are present in all stages, but are by far most abundant in the early stage. While species such as *Bursera simarouba* and *Calycophyllum candidissimun* are most abundant in the late stage. Focusing solely on either of those stages would lead to misleading results about the composition of the forest.

In the early stage there are clearly four dominant families (in terms of the number of individuals) (Table 4.3) that collectively encompass 78.6% of all the individuals. In the more mature stages, this dominance is spread out over a larger number of families, each with fewer individuals. One exception is Fabaceae in the intermediate stage that has 26.5% of the total individuals. In the late stage however, there are six families, each with

abundances within 6% of each other, composing 56.9% of the total abundance. By segregating the results it is possible to see the succession in the species composition of the forest.

*4.4.2 Diversity and Similarity*

The Shannon index assumes that the species were sampled from an indefinitely large population (Pielou 1966) and that all the species are represented in the sample (Magurran 1988). This however is rarely the case in tropical studies (Lieberman and Lieberman 1994). The same problem is apparent in measures of evenness (H` and E) that can give biased results if a large a proportion of species are not sampled. Therefore, in areas as species rich as the tropics an index such as the Brillouin index is more appropriate. It describes the collection of species sampled, and does not extrapolate to the whole population while the Shannon index estimates the diversity of the population as well as the sample. However, the computational simplicity of the Shannon index (in comparison to the Brillouin) has made it more popular (Magurran 1988). Both indices are highest for the intermediate stage. In this transitional stage, the composition of the forest includes species that were pioneers in the regeneration process as well as species indicative of a mature forest.

The disadvantage of the Sørenson index (for β diversity) is that species abundance is not taken into consideration (Magurran 1988). In our study area where there are very few individuals of certain species (ex. 73 species in our entire floristic sample of 159 species are represented by fewer than 5 individuals) the values could be biased. The Morista-Horn index takes into consideration species abundance, but it is influenced by

the abundance of the most abundant species, however, unlike other quantitative indices, it is not affected by sample size or species richness (Magurran 1988). However, both β diversity indices give results consistent with the concept of forest succession. Changes in diversity among the stages are accompanied by changes in dominance where it is shared by an increased number of species in the intermediate stage than in the early or late stages. Segura et al. (2002) found a combination of environmental and biotic conditions play an important role in the determination and maintenance of the diversity in the *T-df*. Similarily, Balvanera et al. (2002) also found that environmental factors determine the variability in abundance, species richness and β diversity at the site level. At the landscape level, Segura et al. (2002) also found β diversity to be strongly linked to gradients in environmental factors such as water availability.

The cluster analysis (Figure 4.5) yielded informative results in terms of fire and past land use history. The fire and land use history and for fifteen plots are illustrated in Table 4.8. Contrary to popular belief, natural fire is not a frequent occurrence in *T-df*s (Hopkins 1983). However, as seen in Table 4.8, anthropogenic fire is one of the most important factors controlling species. For example, similar fire history for sites 1 and 7 or 2 and 10 has a clear influence on the regeneration of the sites. Frequent anthropogenic burning is one of the leading causes of *T-df* conversion to savannah (Hopkins 1983). Grasses such as *Hyparhennia rufa* (L.) invade rapidly after burning at the expense of woody dry forest species. Intense land use (ex. site 4) also alters a site causing the regeneration to be completely different from surrounding areas. In a similar study in the Yucatan, Gonzalez-Iturbe et al. (2002) found that Henequen (*Agave fourcroydes* Lem) plantations greatly influenced the regenerating forest limiting species richness. In

contrast, non-permanent cultivation such as slash and burn agriculture facilitates the regeneration of an increased number of species (Brown and Lugo 1990). If substantiated, this could pose problems for forest regeneration in countries such as Costa Rica where large areas of forest have been cleared for permanent crops like coffee. In addition to fire and land use history, other well-documented factors (i.e. availability of and proximity to seed sources – not investigated in this study) are just as important for determining the species composition of the regenerating forest (Denslow 1996, Gonzalez-Iturbe et al. 2002). Not only does anthropogenic disturbance affect species richness, but it is also partially responsible (along with random thinning, dispersal modes and colonization rates) for a clumped distribution of adult trees among the most common *T-df* species (Hubbell 1979).

*4.4.3 Structure and Complexity*

The fuzzy partitioning analysis assigned each of the 26 sites into all three classes (representing the three stages) with a partial membership to each (fractal memberships). We believe this is more realistic than a hard cluster analysis because the stages are not discrete units but rather a continuum where a particular site has characteristics of more than one stage. The results of the closest hard cluster approximation indicate this overlap. The one early site that had a higher fractal membership to the intermediate cluster is an example of this continuum.

The $C_{HCI}$ provides an objective measure of mature natural forest physiognomy (Holdridge 1967; Holdridge et al. 1971, Ewel 1999). The primary elements of forest physiognomy (H, $G_B$, D, $S_P$) are combined from simple forest measurements in this

index. The inclusion of $S_P$ in $C_{IICI}$ has been contested, however, in principle $S_P$ is a measure of the number of ecological niches, reflected by the variety of life forms, as represented by the number of species (Holdridge et al., 1971). Since this index combines all of the structural data as well as the number of species and the density of stems, the changes in this index through time as the forest matures is an indication of the changes in forest physiognomy.

*4.4.4 Leaf Area Index*

Two trends are apparent in the box plots in Figure 4.7. The first is that in the wet season, LAI increases with successional stage even though there is a large overlap in the range of values between all seasons. The second is an increase in the dry season LAI from the early to the intermediate stage and then a subsequent decrease to the late stage. Assuming a completely leafless canopy, the dry season LAI values from Table 4.7 are shown as the %WAI (wood-area-index). Plots with the highest values of WAI could suggest that there is a prevalence of thick lianas or other woody matter. This is alluded to in the leaf litter data. However, values of %WAI in excess of 30% suggest that there are either species practicing reverse phenology (i.e. *J. nervosa*) or that the canopy is not completely leafless in those plots. The contour plots in Figure 4.8 substantiate a contribution of leaves to the values termed %WAI in Table 4.7.

The large overlap in LAI values between stages is also visible in Figure 4.9 where LAI resembles a continuum similar to the one seen in the physiognomic characteristics. An asynchronous leaf phenological cycle is apparent for the three stages. However, the difference in phase is most pronounced in the intermediate stage. During different months

of the year, it is indistinguishable from either the early or the late stage. Such an asynchronicity could have important implications at a regional level if LAI is being extracted from remotely sensed data. Time of image acquisition is always a concern in the *T-df* (Chapter 2), but depending on the goals of a study, the accuracy of derived LAI values may differ with respect to time. This also shows the need for multi-temporal image analysis because examination of LAI – remotely sensed data relationships at a given time could lead to confusion. With respect to biogeochemical models that require LAI as an input (ex. CENTURY) (Parton et al. 1997, Pfaff et al. 2000) these differences in phase in the seasonal LAI cycles show the importance of examining a forest cover segregated by successional stage.

Apart from empirical models, another way to infer LAI taking into consideration the asynchronous leaf phenological cycles of the three successional stages is through a Bayesian network. Figure 4.11 illustrates the simplest example of a possible Bayesian network that could be used in this case. In the example in Figure 4.11, LAI has two parental nodes (successional stage and month of the year). The conditional probability table for LAI is a simple combination of all the possible combinations of stage and month where the probability of LAI being one of the 8 LAI categories is the probability from the frequency distribution at each particular stage and month combination. With inference engines it is then possible to compute what the probability is of LAI being a certain value given the successional stage and the month.

## 4.5. Conclusions

- Species richness is the greatest in the intermediate stage followed by the late and then the early stage.
- Past land use history, land use intensity and the frequency of anthropogenic disturbances clearly influences species composition and the structure of regenerating canopy.
- Successional stages can be statistically distinguished based on general physiognomic measurements.
- The structural changes of the tropical dry forest as it progresses through successional stages can be quantified by a modification of the Holdridge Complexity Index.
- Seasonal changes in LAI in the different successional stages are asynchronous. With the greatest difference being in the intermediate stage
- The applicability of the results from this study to other *T-df* environments needs to be substantiated through comparative studies with other *T-df*s.

## 4.6. References

Abbell M.L., Braselton J.P., and Rafter J.A. 1998. Statistics with Mathematica. Academic Press, Toronto.

Arroyo-Mora, P. 2002. Forest cover assessment, fragmentation analysis and secondary forest detection for the Chorotega Region, Costa Rica. Master of Science. University of Alberta, Edmonton.

Balvanera P., Lott E., Segura G., Siebe C., and Islas A. 2002. Patterns of B diversity in a Mexican tropical dry forest. Journal of Vegetation Science **13**:145-158.

Brown S., and Lugo A.E. 1990. Tropical Secondary Forest. Journal of Tropical Ecology **6**:1-32.

Burnham R.J. 1997. Stand characteristics and leaf litter composition of a dry forest hectare in Santa Rosa National Park, Costa Rica. Biotropica **29**:387-395.

Chazdon R.L., and Denslow J. 2002. Floristic Composition and Species Richness. Pages 513-522 *in* Chazdon R.L and Whitmore T.C., editors. Foundations of Tropical Forest Biology. Classic Papers with Commentaries. University of Chicago Press, Chicago, IL.

Chen J.M., and Cihlar J. 1995. Quantifying the effect of canopy architecture on optical measurements of leaf area index using two gap size analysis methods. IEEE Transactions on Geoscience and Remote Sensing **33**:777-787.

Chen J.M. 1996. Evaluation of vegetation indices and a modified simple ratio for Boreal applications. Canadian Journal of Remote Sensing **22**:229-241.

Chen J.M., Rich P.M., Gower S.T., Norman J.M., and Plummer S. 1997. Leaf area index of boreal forests: Theory, techniques and measurements. Journal of Geophysical Research **102**:24429-24443.

Cohen W.B., T. K. Maiersperger, Gower S.T., and Turner D.P. 2003. An improved strategy for regression of biophysical variables and Landsat ETM+ data. Remote Sensing of Environment **84**:561-571.

Denslow J. 1996. Functional group diversity and responses to disturbance. *in* Orians G. and et al., editors. Biodiversity and Ecosystem Processes in Tropical Forest. Springer.

Diggle P.J. 1983. Statistical Analysis of spatial point patterns. Academic Press.

NewYork.

Ewel J.J. 1999. Natural systems as models for the design of sustainable systems of land use. Agroforestry Systems **45**:1-21.

Fernandes R.F., Butson C., Leblanc S.G., and Latifovic R. 2003. Landsat-5 TM and Landsat-7 ETM+ based accuracy assessment of leaf area index products for Canada derived from SPOT-4 VEGETATION data. Canadian Journal of Remote Sensing **29**:241-258.

Fischer A.G. 1960. Latitudinal variations in organic diversity. Evolution **14**:64-81.

Fournier R.A., Mailly D., Walter J.-M.N., and Soudani K. 2003. Measurement of Forest Structure. *in* Wulder M. and Franklin S, editors. Methods for Remote Sensing of Forests: Concepts and Case Studies. Kluwer Academic Press.

Freeman E.A., and Ford E.D. 2002. Effects of data quality on analysis of ecological pattern using the K(d) statistical function. Ecology **83**:35-46.

Gentry A.H. 1982. Neotropical floristic diversity: phytographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Annals of the Missouri Botanical Garden **69**:557-593.

Gentry A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden **75**:1-34.

Gentry A.H. 1995. Diversity and floristic composition of neotropical dry forests. Pages 146-194 *in* Mooney H.A., Bullock S.H., and Medina E., editors. Seasonally Tropical Forests. University of Cambridge Press, Cambridge.

Gillespie T.W., Grijalva A., and Farris C.N. 2000. Diversity, composition and structure

of tropical dry forests in Central America. Plant Ecology **147**:37-47.

Giulietti A.M., and Pirani J.R. 1988. Patterns of geographic distribution of some plant species from the Espinhaço Range, Minas Gerais and Bahia, Brazil. Pages 39-69 *in* Vanzolini P.E. and Heyer W.R., editors. Proceedings of a workshop on neotropical distribution patterns. Academia Brasileira de Ciências, Rio de Janeiro, Brazil.

Gonzalez-Iturbe J.A., Olmsted I., and Tun-Dzul F. 2002. Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico. Forest Ecology and Management **167**.

Goward S.N., Markham B., Dye D.G., Dualney W., and Yand J. 1991. Normalized difference vegetation index measurements for the Advanced Very High Resolution Radiometer. Remote Sensing of Environment **35**:257-277.

Hartshorn G.S. 1983. Plants. Pages 118-157 *in* Janzen D.H., editor. Costa Rican Natural History. University of Chicago Press, Chicago.

Holbrook N.M., Whitbeck J.L., and Mooney H.A. 1995. Drought responses of neotropical dry forest trees. Pages 243-276 *in* Mooney H.A., Bullock S.H., and Medina E., editors. Seasonally Tropical Forests. University of Cambridge Press, Cambridge.

Holdridge L. 1967. Life Zone Ecology. Tropical Science Center, San Jose, Costa Rica.

Holdridge L., Grenke W.C., Hatheway W.H., Liang T., and Tosi J.Jr. 1971. Forest Environments in Tropical Life Zones: A Pilot Study. Pergamon Press, New York.

Hopkins B. 1983. Successional processes. Pages 605-616 *in* Bourliere F., editor. Tropical Savannas. Elsevier, New York.

Hubbell S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science **203**:1299-1309.

Janzen D.H., and Liesner R. 1980. Annotated checklist of lowland Guanacasts Province, Costa Rica, exclusive of grasses and nonvascular cryptograms. Brenesia **18**:15-90.

Janzen D.H., editor. 1983. Costa Rican Natural History. University of Chicago Press, Chicago.

Janzen D.H. 1986. Tropical dry forests: the most endangered major tropical ecosystem. Pages 130-137 *in* Wilson E.O., editor. Biodiversity. National Academy Press, Washington.

Janzen D.H. 1988. Management of habitat fragments in a tropical dry forest: Growth. Annals of Missouri Botanical Garden **75**:105-116.

Janzen D.H. 1993. Caterpillar seasonality in a Costa Rican dry forest. Pages 448-477 *in* Stamp N.E. and Casey T.M., editors. Caterpillars: Ecological and evolutionary constraints on foraging. Chapman and Hall, New York.

Joly A.B. 1970. Conheça a vegetação brasileira. EDUSP e Polígono, São Paulo, Brazil.

Kauffman J.B., Steele M.D., Cummings D.L., and Jaramillo V.J. 2002. Biomass dynamics associated with deforestation, fire, and, conversion to cattle pasture in a Mexican tropical dry forest. Forest Ecology and Management **59**:1-12.

Leblanc S., and Chen J.M. 2001. A practical scheme for correcting multiple scattering effects on optical LAI measurements. Agricultural and Forest Meteorology **110**:125-139.

LI-COR Inc. 1992. LAI-2000 Plant Canopy Analyzer Instruction/Operating Manual. LI-COR Inc., Lincoln, NE.

Lieberman M., and Lieberman D. 1994. Patterns of diversity and dispersion of forest trees. Pages 106-119 *in* McDade L.A., Bawa K.S., Hespenheide H.A., and Hartshorn G.S., editors. La Selva. University of Chicago Press, Chicago.

Lott E. 1985. Listados floristicos de Mexico III. La Estacion de Biologia Chamela, Jalisco. Instituto de Biologia, Universidad Nacional Autonoma de Mexico, Mexico.

Lugo A.E., Gonzalez-Liboy J.A., Cintron B., and Dugger K. 1978. Structure, productivity and transpiration of a subtropical dry forest in Puerto Rico. Biotropica **10**:278-291.

Luttge U. 1997. Physiological Ecology of Tropical Plants. Springer-Verlag.

Maass M. 1995. Conversion of tropical dry forest to pasture and agriculture. Pages 399-422 *in* Mooney H.A., Bullock S.H., and Medina E., editors. Seasonally Tropical Forests. University of Cambridge Press, Cambridge.

Magurran A.E. 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, NJ.

Martinez-Yrizar A., and Sarukhan J. 1990. Litterfall patterns in a tropical deciduous forest in Mexico over a five-year period. Journal of Tropical Ecology **6**:433-444.

Medina E. 1995. Diversity of life forms of higher plants in neotropical dry forests. Pages 221-242 *in* Bullock S.H., Mooney H.A., and Medina E., editors. Seasonally Tropical Forests. Cambridge University Press, Cambridge.

Mooney H.A., Bullock S.H., and Medina E. 1995. Introduction. Pages 1-8 *in* Mooney H.A., Bullock S.H., and Medina E., editors. Seasonally Tropical Forests. Cambridge University Press, Cambridge.

Murphy P.G., and Lugo A.E. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica **18**:89-96.

Murphy P.G., and Lugo A.E. 1995. Dry forests of Central America and the Caribbean. Pages 9-34 *in* Mooney H.A., Bullock S.H., and Medina E., editors. Seasonally Tropical Forests. University of Cambridge Press, Cambridge.

Parton W.J., Schimel. D.S., Cole C.V., and Ojima D.S. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal **51**:1173-1179.

Pfaff A.S.P., Kerr S., Hughes F., Liu S., Sanchez-Azofeifa G.A., Schimel D., Tosi J., and Watson V. 2000. The Kyoto protocol and payments for tropical forests: An interdisciplinary method for estimating carbon-offset supply and increasing the feasibility of a carbon market under the CDM. Ecological Economics **35**:203-221.

Pielou E.C. 1966. Species diversity and pattern diversity in the study of ecological reserves. Journal of Theoretical Biology **10**:370-383.

Planchais I., and Pontailler J.-Y. 1999. Validity of leaf areas and angles estimated in a Beech forest from analysis of gap frequencies, using hemispherical photographs and a plant canopy analyzer. Annals of Forest Science **56**:1-10.

Quigley M.F., and Platt W.J. 2003. Composition and structure of seasonally deciduous forests in the Americas. Ecological Monographs **7**:87-106.

Ripley D. 1976. The second-order analysis of stationary point processes. Journal of applied probability **13**:255-266.

Running S.W., Peterson D.L., Spanner M.A., and Teuber K.B. 1986. Remote sensing of coniferous forest leaf area. Ecology **67**:273-276.

Rzedowski J. 1991. El endemismo en la flora fanerogamica mexicana: una apreciacion analitica preliminar. Acta Botanica Mexicana **15**:47-64.

Segura G., Balvanera P., Duran E., and Perez A. 2002. Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest. Plant Ecology **00**:1-13.

Struyf A., Hubert M., and Rousseeuw P.J. 1997. Integrating Robust Clustering Techniques in S-PLUS. Computational Statistics and Data Analysis **26**:17-37.

Turner D.P., Cohen W.B., Kennedy R.E., Fassnacht K.S., and Briggs J.M. 1999. Relationships between leaf area index and Landsat TM spectral vegetation indices across three temperate zone sites. Remote Sensing of Environment **70**:52-68.

Walter H. 1971. Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh.

Welles J.M. 1990. Some indirect methods of estimating canopy structure. Remote Sensing Reviews **5**:31-43.

Welles J.M., and Norman J.M. 1991. An instrument for direct measurement of canopy architecture. Agronomy Journal **83**:818-825.

Welles J.M., and Cohen S. 1996. Canopy structure measurement by gap fraction analysis using commercial instrumentation. Journal of Experimental Biology **47**:1335-1342.

## APPENDIX I

| | |
|---|---|
| $a$ | number of species in site A |
| $A$ | area |
| $an_i$ | number of individuals of the ith species in site A |
| $aN$ | number of individuals in site A |
| $b$ | number of species in site B |
| $bn_i$ | number of individuals of the ith species in site B |
| $bN$ | number of individuals in site B |
| $C_{HCI}$ | Holdridge Complexity Index |
| $C_j$ | Jaccard Index |
| $C_{MH}$ | Morista-Horn Index |
| $C_S$ | Sørenson Index |
| $D$ | Density |
| $E$ | Evenness |
| $G$ | fraction of foliage projected towards $(\theta,\Phi)$ |
| $G_b$ | basal area |
| $H$ | height |
| $H`$ | Shannon index |
| $HB$ | Brillouin index |
| $HB_{max}$ | maximum possible diversity |
| $j$ | number of species common to both sites A and B |
| $K$ | extinction coefficient |
| $L$ | leaf area index |
| $L_f$ | foliar leaf area index |
| $LAI_e$ | effective leaf area index |
| $n_i$ | number of species |
| $N$ | number of individuals |
| $NDVI$ | normalized difference vegetation index |
| $p_i$ | proportional abundance of the ith species |
| $S$ | path length through canopy |
| $S_p$ | total number of species |
| $T$ | probability of non-interception |
| $\alpha$ | ratio between the projected area of material other than foliage over total projected area |
| $\theta$ | zenith angle |
| $\mu$ | foliage density |
| $\rho_{NIR}$ | near infrared reflectance |
| $\rho_{Red}$ | red reflectance |
| $\Upsilon_E$ | aggregation at the shoot level |
| $\Phi$ | azimuth angle |
| $\Omega_E$ | aggregation at all levels coarser than shoot level |
| $\zeta$ | diameter at breast height |

Table 4.1 Dates of LAI collection, Santa Rosa National Park

| Season | Collection Date |
|---|---|
| End of wet season | December 2001 |
| Dry season | February 2002 |
| End of dry season | May 2002 |
| Beginning of wet season | August 2002 |
| Wet Season | September 2002 |
| Wet Season | November 2002 |
| End of wet season | December 2002 |
| Beginning of dry season | January 2003 |
| Dry season | April 2003 |

Table 4.2. List of woody species (DBH > 5cm) identified in the three different successional stages in Santa Rosa National Park

| Family | Species | Early Stage | Intermediate Stage | Late Stage |
|---|---|---|---|---|
| Anacardiaceae | *Astronium graveolens* (Jacq.) | | X | X |
| | *Spondias mombin* (L.) | X | X | X |
| | *Spondias purpurea* (L.) | X | X | |
| Annonaceae | *Annona holosericea* (Saff.) | | X | |
| | *Annona purpurea* (Moc. & Sesse) | | X | X |
| | *Annona reticulata* (L.) | | X | X |
| | *Desmopsis bibracteata* (Saff.) | | X | |
| | *Sapranthus palanga* (R.E.Fr.) | X | X | X |
| Apocynaceae | *Forsteronia spicata* (Jacq.) | X | | |
| | *Stemmadenia obovata* (Hook & Arn.) | | X | X |
| | *Thevetia ovata* (Cav.) | X | | |
| Araliaceae | *Sciadodendron excelsum* (Griseb.) | X | X | |
| Asteraceae | *Lasianthaea fruticosa* (L.) | X | | |
| Bignonaceae | *Amphilophium paniculatum* (L.) | | X | X |
| | *Arrabidaea mollissima* (Kunth) | | X | X |
| | *Crescentia alata* (Kunth) | X | | |
| | *Cydista diversifolia* (Kunth) | | X | |
| | *Cydista heterophylla* (Seibert) | | X | |
| | *Mansoa hymenaea* (DC.) | | X | |
| | *Tabebuia impetiginosa* (Mart.) | | X | |
| | *Tabebuia ochracea* (Cham.) | X | X | X |
| | *Tabebuia rosea* (Bertol.) | | | X |
| Bombacaceae | *Bombacopsis quinata* (Jacq.) | | X | X |
| Boraginaceae | *Cordia alliodora* (Ruiz & Pav.) | X | X | X |
| | *Cordia dentata* (Poir) | X | | |
| | *Cordia guanacastensis* (Standl) | | X | |
| | *Cordia panamensis* (L. Riley) | | X | X |
| Burseraceae | *Bursera simarouba* (L.) | X | X | X |
| | *Bursera tomentosa* (Jacq.) | X | X | X |
| Capparidaceae | *Capparis indica* (L.) | | X | |
| Cecropiaceae | *Cecropia peltata* (L.) | X | X | X |
| Celastraceae | *Maytenus segoviarum* (Standl. & Steyerm.) | | X | X |
| Chrysobalanaceae | *Hirtella racemosa* (Lam) | | X | X |
| | *Licanea arborea* (Seem.) | | X | X |
| Clusiaceae | *Vismia baccifera* (L.) | | | X |
| Cochlospermaceae | *Cochlospermum vitifolium* (Willd.) | X | X | X |
| Combretaceae | *Combretum decandrum* (Jacq.) | | X | |
| | *Combretum farinosum* (Kunth) | X | | |
| Connaraceae | *Rourea glabra* (Kunth) | | X | |
| Dilleniaceae | *Curatella americana* (L.) | X | X | |
| | *Tetracera volubilis* (L.) | | X | X |
| Ebenaceae | *Diospyros salicifolia*(Willd.) | X | X | X |
| Elaeocarpaceae | *Sloanea terniflora* (Moc. & Sesse) | | | X |
| Erythroxylaceae | *Erythroxylum havanense* (Jacq.) | | X | X |
| | *Erythroxylum rotundifolium* (Lunan) | X | | |

| | | | | |
|---|---|---|---|---|
| Euphorbiaceae | *Croton niveus* (Jacq.) | X | X | |
| | *Euphorbia schlechtendalii* (Boiss) | X | X | |
| | *Jatropha curcas* (L.) | | | X |
| | *Margaritaria nobilis* (L.f.) | | | X |
| | *Sapium glandulosum* (L.) | | X | X |
| | *Sebastiana pavonia* (Mull. Arg.) | | X | X |
| Fabaceae – Caesalpinioideae | *Bahuinia ungulata* (L.) | X | X | X |
| | *Hymenaea courbaril* (L.) | | X | X |
| | *Senna atomaria* (L.) | X | X | |
| Fabaceae – Mimosoideae | *Acacia collinsii* (Saff.) | X | X | |
| | *Albizia adinocephala* (Donn. Sm.) | | X | |
| | *Albizia nipoides* (Spruce) | | X | X |
| | *Enterolobium cyclocarpum* (Jacq.) | X | | X |
| | *Inga vera* (Willd) | | | X |
| | *Lysiloma auritium* (Schltdl) | X | X | X |
| | *Lysiloma divaricatum* (Jacq.) | | X | X |
| | *Mimosa acantholoba* (Humb. & Bonpl) | | X | |
| | *Mimosa tricephala* (Cham&Schltdl) | X | | |
| | *Piptadenia flava* (Spreng) | X | X | X |
| | *Pithecellobium lanceolatum* (Humb. & Bonpl.) | X | X | |
| | *Samanea saman* (Jacq.) | | X | X |
| Fabaceae – Papilionoideae | *Acosmium panamense* (Benth.) | | X | X |
| | *Ateleia herbert-smithii* (Pittier) | X | X | X |
| | *Dalbergia retusa* (Hemsl.) | X | X | |
| | *Dioclea violacea* (Mart) | X | | |
| | *Diphysa Americana* (Mill.) | X | | |
| | *Gliricidia sepium* (Jacq.) | X | X | X |
| | *Lonchocarpus felipei* (N. Zamora) | X | X | X |
| | *Lonchocarpus minimiflorus* (Donn. Sm.) | | X | X |
| | *Lonchocarpus parviflorus* (Benth.) | | X | |
| | *Lonchocarpus phlebophyllus* (Standl. & Steyerm.) | X | X | |
| | *Lonchocarpus rugosus* (Benth.) | X | | X |
| | *Machaerium biovulatum* (Micheli) | X | X | X |
| | *Myrospermum frutescens* (Jacq.) | | X | |
| | *Platymiscium pleiostachyum* (Donn. Sm.) | | X | |
| | *Swartzia cubensis* (Britton & P.Wilson) | | | X |
| Fagaceae | *Quercus oleoides* (Schltdl. & Cham.) | X | | X |
| Flacourtiaceae | *Casearia aculeate* (Jacq.) | | X | |
| | *Casearia arguta* (Kunth) | X | X | |
| | *Casearia corymbosa* (Kunth) | X | X | X |
| | *Casearia sylvestris* (Sw.) | X | X | X |

| | | | | |
|---|---|---|---|---|
| | *Prockia crucis* (P. Browne) | X | X | |
| | *Xylosoma flexuosa* (Kunth) | | X | |
| | *Zuelania guidonia* (Sw.) | | | X |
| Hippocrateaceae | *Hippocratea volubilis* (L.) | | | X |
| | *Semialarium mexicanum* (Miers) | X | X | X |
| Lauraceae | *Ocotea veraguensis* (Meisn) | | | X |
| Malpighiaceae | *Bunchosia biocellata* (Schlecht) | | X | X |
| | *Byrsonima crassifolia* (L.) | X | X | |
| Malvaceae | *Malvaviscus arboreus* (Cav.) | | | X |
| Melastomataceae | *Miconia argentea* (Sw.) | | X | X |
| Meliaceae | *Cedrela odorata* (L.) | X | X | |
| | *Guarea glabra* (Vahl) | | | X |
| | *Swietenia macrophylla* (King) | X | X | X |
| | *Trichilia americana* (Sesse & Moc) | | X | |
| | *Trichilia glabra* (L.) | | X | X |
| Moracea | *Brosimum alicastrum* (Sw.) | | | X |
| | *Castilla elastica* (Sesse) | | X | X |
| | *Ficus cotinifolia* (Kunth) | | X | |
| | *Maclura tinctoria* (L.) | | X | X |
| Myrsinaceae | *Ardisia revolute* (Kunth) | X | | X |
| Myrtaceae | *Eugenia salamensis* (Donn.Sm.) | | X | X |
| Nyctaginaceae | *Pisonia aculeata* (L.) | | X | X |
| Olacaceae | *Schoepfia schreberi* (J.F.Gmel.) | X | X | X |
| Opiliaceae | *Agonandra macrocarpa* (L.O.Williams) | | | X |
| Polygalaceae | *Securidaca sylvestris* (Schltdl.) | | | X |
| Polygonaceae | *Coccoloba venosa* (L.) | | X | X |
| Rhamnaceae | *Gouania polygama* (Jacq.) | X | | |
| | *Karwinskia calderonii* (Standl.) | X | X | |
| Rubiaceae | *Calycophyllum candidissimum* (Vahl) | | X | X |
| | *Chomelia spinosa* (Jacq.) | | X | X |
| | *Exostema mexicanum* (A. Gray) | | X | X |
| | *Genipa americana* (L.) | X | X | X |
| | *Guettarda macrosperma* (Donn.Sm.) | | X | X |
| | *Hamelia patens* (Jacq.) | | | X |
| | *Randia armata* (Sw.) | | X | |
| | *Randa monantha* (Benth.) | X | X | X |
| | *Randia thurberi* (S. Watson) | X | | X |
| Rutaceae | *Zanthoxylum setulosum* (P. Wilson) | | | X |
| Sapindaceae | *Allophylus occidentalis* (Sw.) | | X | |
| | *Cupania guatemalensis* (Turcz.) | | | X |
| | *Dilodendron costaricense*(Radlk) | | | X |
| | *Serjania mexicana* (L.) | | X | X |
| | *Thouinidium decandrum* (Humb. & Bonpl.) | | X | X |
| Sapotaceae | *Manilkara chicle* (Pittier) | X | X | X |
| | *Sideroxylon capiri* (A. DC.) | | X | |
| | *Chrysophylum brenesii* (Cronquist) | | | X |
| Simaroubaceae | *Picramnia antidesma* (Sw.) | | | X |

| | | | | |
|---|---|---|---|---|
| | *Simarouba glauca* (DC.) | | X | X |
| Solanaceae | *Solanum hazenii* (Britton) | | X | |
| Sterculiaceae | *Guazuma ulmifolia* (Lamarck) | X | X | X |
| Theophrastaceae | *Jacquinia nervosa* (C. Presl.) | | X | X |
| Tiliaceae | *Apeiba tibourbou* (Aubl.) | X | X | X |
| | *Luehea candida* (DC.) | X | X | X |
| | *Luehea speciosa* (Willd.) | X | X | X |
| Trigoniaceae | *Trigonia rugosa* (Benth.) | X | | |
| Verbenaceae | *Aegiphila panamensis* (Moldenke) | | X | |
| | *Cornutia grandifolia* (Schltdl. & Cham.) | | X | |
| | *Lippia cardiostegia* (Benth.) | X | | |
| | *Rehdera trinervis* (S.F. Blake) | X | X | X |

Table 4.3 Families with a % composition greater than 5% in the three successional stages.

| Stage | Family | % composition | No. of species |
|---|---|---|---|
| Early | Cochlospermaceae | 13.7 | 1 |
| | Fabaceae | 21.2 | 17 |
| | Sterculiaceae | 18.5 | 1 |
| | Verbenaceae | 25.2 | 2 |
| Intermediate | Boraginaceae | 07.8 | 3 |
| | Cochlospermaceae | 05.0 | 1 |
| | Euphorbiaceae | 05.0 | 4 |
| | Fabaceae | 26.4 | 23 |
| | Rubiaceae | 07.3 | 7 |
| | Tiliaceae | 05.6 | 3 |
| Late | Burseaceae | 05.3 | 2 |
| | Euphorbiaceae | 11.3 | 4 |
| | Fabaceae | 11.7 | 17 |
| | Hippocrataceae | 09.5 | 2 |
| | Rubiaceae | 10.8 | 8 |
| | Sapindaceae | 08.3 | 4 |

Table 4.4 Brillouin and Shanon Diversity Indices and their respective measures of evenness.

| Stage | Brillouin Index (HB) | HB Evenness | Shannon Index (H`) | H` Evenness |
|---|---|---|---|---|
| Early | 2.56 | 0.424 | 2.66 | 0.378 |
| Intermediate | 3.91 | 0.647 | 4.08 | 0.581 |
| Late | 3.68 | 0.653 | 3.88 | 0.586 |

Table 4.5 Morista-Horn and Sørenson similarity indices.

| Stage | Morsita-Horn Index | Sørenson Index |
|---|---|---|
| Early – Intermediate | 0.30 | 0.55 |
| Intermediate – Late | 0.52 | 0.64 |
| Early – Late | 0.26 | 0.46 |

Table 4.6 Mean values with one standard deviation of the forest structural characteristics (height, basal area, density and number of species) along with the Holdridge Complexity Index, a measure of forest physiognomy.

| Stage | Height | Basal Area | Density | Species | HCI |
|---|---|---|---|---|---|
| Early | 7.5±2.2 | 11.7±5.4 | 112±64 | 15±7 | 28.0±36.0 |
| Intermediate | 10.3±3.4 | 21.4±6.8 | 130±35 | 29±5 | 68.6±33.7 |
| Late | 15.0±2.2 | 30.1±6.5 | 107±42 | 29±7 | 159.0±57.7 |

*Height is measured in meters, basal area in $m^2$/hectare, density in number of stems and species as the number of species. HCI is unit less.

Table 4.7 Maximum and minimum mean LAI values for each plot along with the ratio of the possible contribution of the Wood-area-index (WAI) represented by α and HCI for comparison. *WAI is hypothetical, assuming the Min LAI values represent a completely leafless canopy. §Holdridge Complexity Index (HCI) values are included as a description of plot physiognomy.

| Stage | Max LAI | Min LAI | α* | HCI§ |
|---|---|---|---|---|
| E | 0.6 | 0.2 | 0.32 | 0.5 |
| E | 1.9 | 0.5 | 0.25 | 5.7 |
| E | 2.5 | 0.8 | 0.33 | 17.3 |
| E | 3.0 | 0.6 | 0.19 | 31.2 |
| E | 3.2 | 1.3 | 0.42 | 19.9 |
| E | 4.3 | 0.9 | 0.20 | 49.9 |
| E | 5.3 | 0.2 | 0.05 | 121.1 |
| I | 1.7 | 0.3 | 0.20 | 91.7 |
| I | 2.2 | 1.8 | 0.80 | 129.8 |
| I | 2.6 | 0.9 | 0.34 | 58.3 |
| I | 3.2 | 1.0 | 0.30 | 47.6 |
| I | 4.0 | 0.9 | 0.22 | 27.4 |
| I | 4.6 | 1.0 | 0.21 | 64.7 |
| L | 3.6 | 1.2 | 0.34 | 114.7 |
| L | 5.1 | 0.5 | 0.10 | 229.3 |
| L | 6.6 | 2.7 | 0.42 | 136.7 |

Table 4.8 Land use and anthropogenic fire history of the sites with most similar species composition based on the agglomerative hierarchical cluster analysis.

| Stage | Site | Longitude* | Latitude* | Past land use and anthropogenic fire events |
|---|---|---|---|---|
| Early | 1 | 654336 | 1201976 | Burned 1986 fire |
| Early | 7 | 653142 | 1201759 | Burned 1986 fire |
| Early | 2 | 653407 | 1201921 | Frequent anthropogenic fire |
| Early | 10 | 649113 | 1197383 | Frequent anthropogenic fire |
| Early | 3 | 649870 | 1198971 | Burned completely 1975-1980 – very few seed sources |
| Early | 6 | 650861 | 1198053 | Trees cut in the past, seed sources from remnant trees nearby |
| Early | 4 | 650438 | 1197890 | Grassland in the 40's, inland rice in the 60's, cattle ranch in the 70's, burned clean in 1982-1983 |
| Intermediate | 11 | 651419 | 1197470 | Pastureland in the past |
| Intermediate | 12 | 651794 | 1199823 | Protected by cliff face, abundance of seed sources |
| Intermediate | 14 | 650042 | 1197936 | Light fire 1975-1980 at ground level. Never totally cleared. Timber extraction from 1800's - 1940 |
| Intermediate | 15 | 649650 | 1197722 | Light fire 1975-1980 at ground level. Never totally cleared. Timber extraction from 1800's - 1940 |
| Late | 22 | 651875 | 1199377 | Cleared in 1920's for a banana plantation |
| Late | 21 | 651467 | 1198286 | Previous *Quercus* spp. dominated forest. Valuable timber extracted and subsequently burned. |
| Late | 23 | 647776 | 1194113 | Past human indigenous settlement |
| Late | 24 | 652134 | 1199783 | Relatively undisturbed remnant T-df |

*Latitude and longitude are in UTM zone 16 WGS84 coordinates (m)

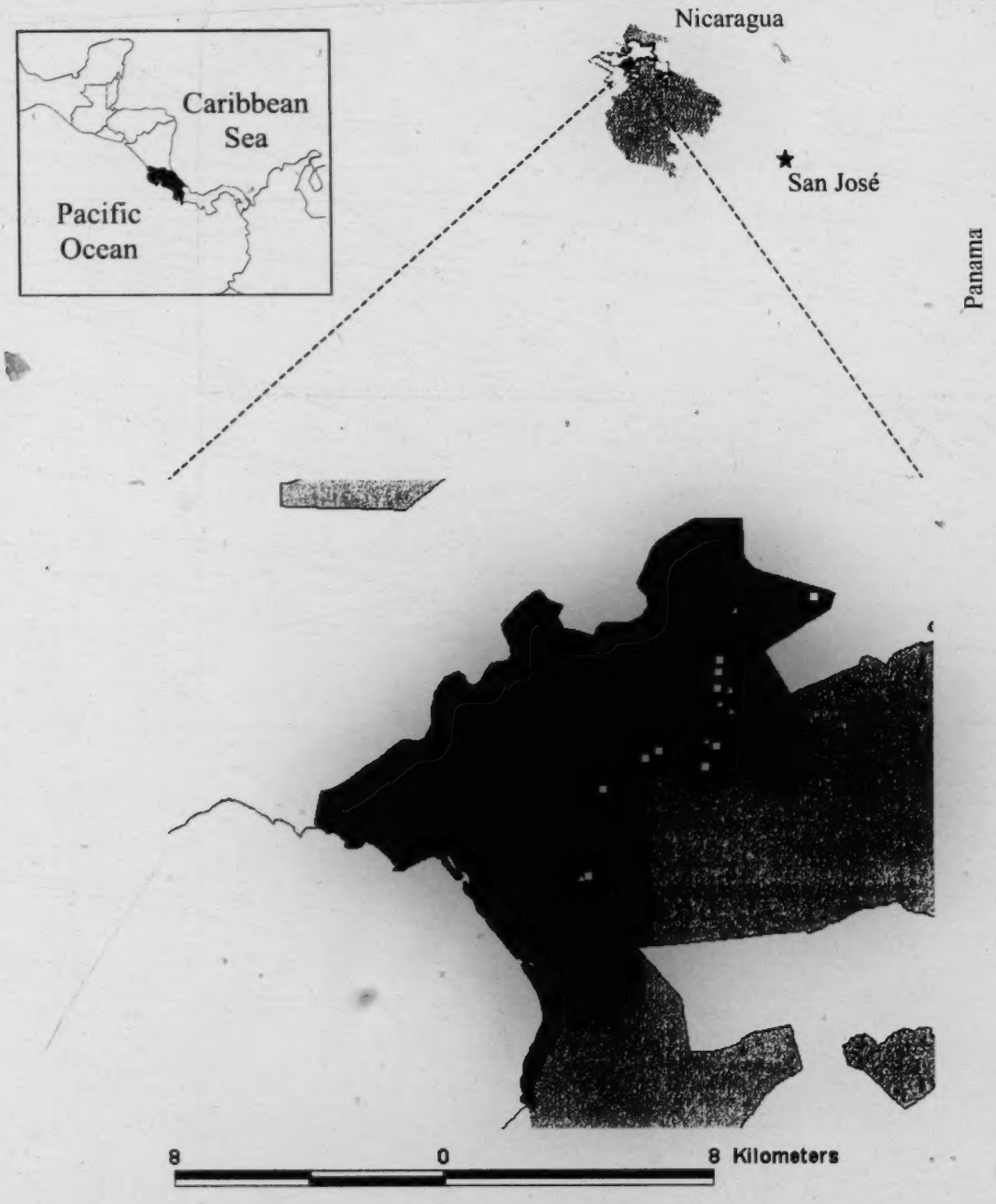



Figure 4.1. Locations of all early (circle), intermediate (square) and late (triangle) plots in the Santa Rosa sector (green) of the Guanacaste Conservation Area (beige), Costa Rica (dark gray).

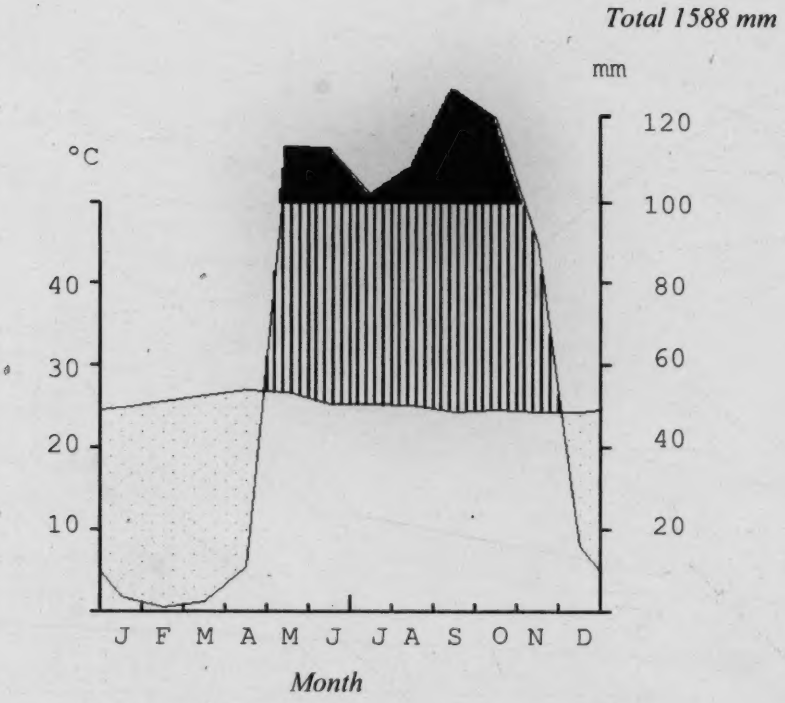



Figure 4.2: Climate diagram for Santa Rosa National Park, Costa Rica. The mean monthly temperature (°C) and the monthly precipitation (mm) are scaled to represent the potential evapotranspiration. Dry months are represented by the dotted areas, humid months by the vertical lines and months with rain in excess of 100mm are in solid black. Diagram created with ECD, Haase 2000.

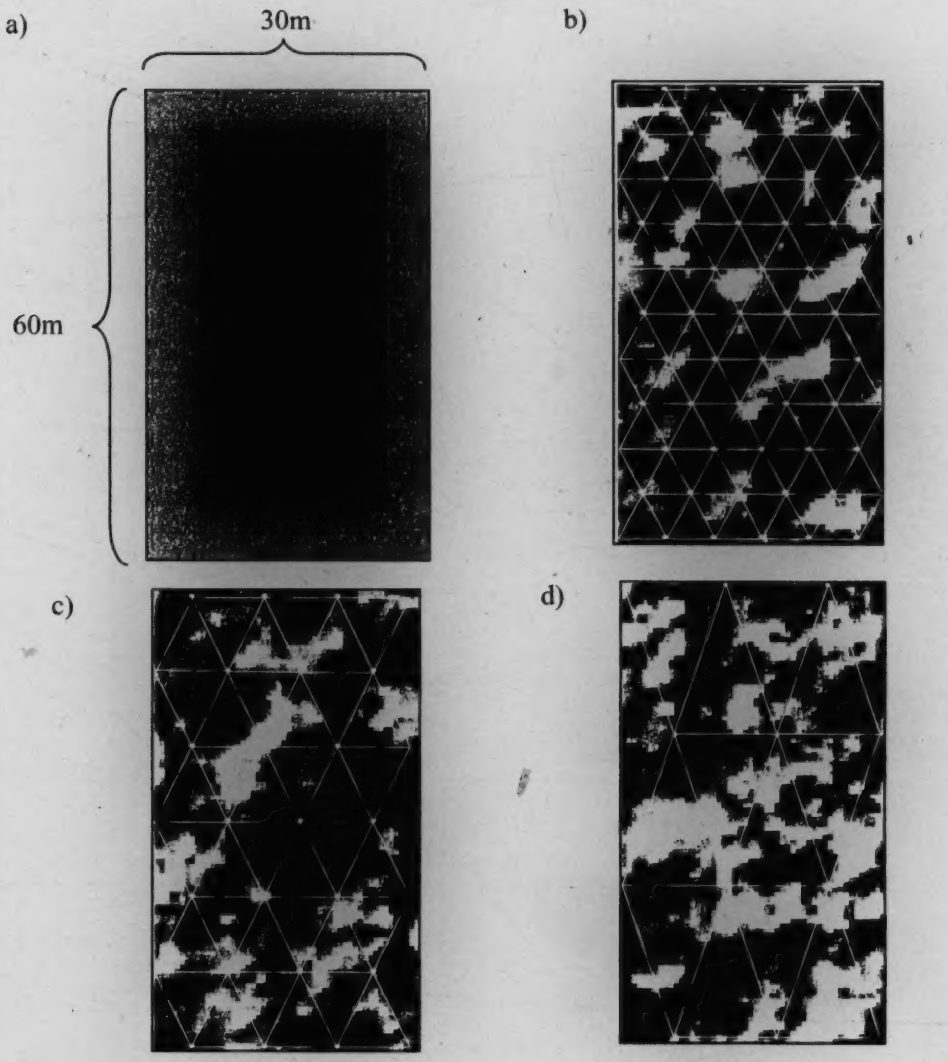



Figure 4.3 Quickbird panchromatic band (0.6m spatial resolution) merged with Quickbird multispectral band (2m spatial resolution) example of each successional stage with LAI sampling scheme superimposed. LAI measurements were taken at the apex of each triangle in the direction of the long axis. a)sampling plot sizes for LAI measurements (light green) and structural variables (dark green) b)early c)intermediate d)late

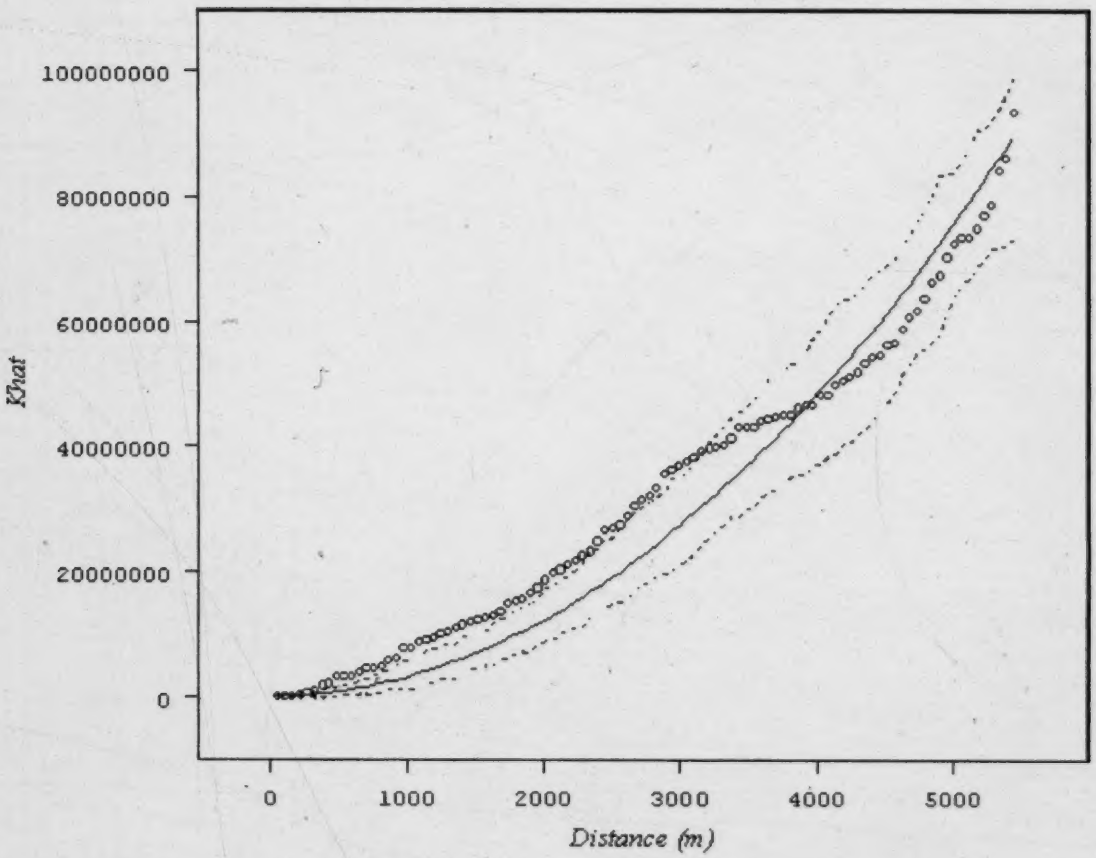



Figure 4.4. Ripley's K function for a spatial point pattern. Solid line indicates the mean for a random distribution, dashed lines indicate the 95% confidence intervals. Open circles represent each of the 100 scales simulated.

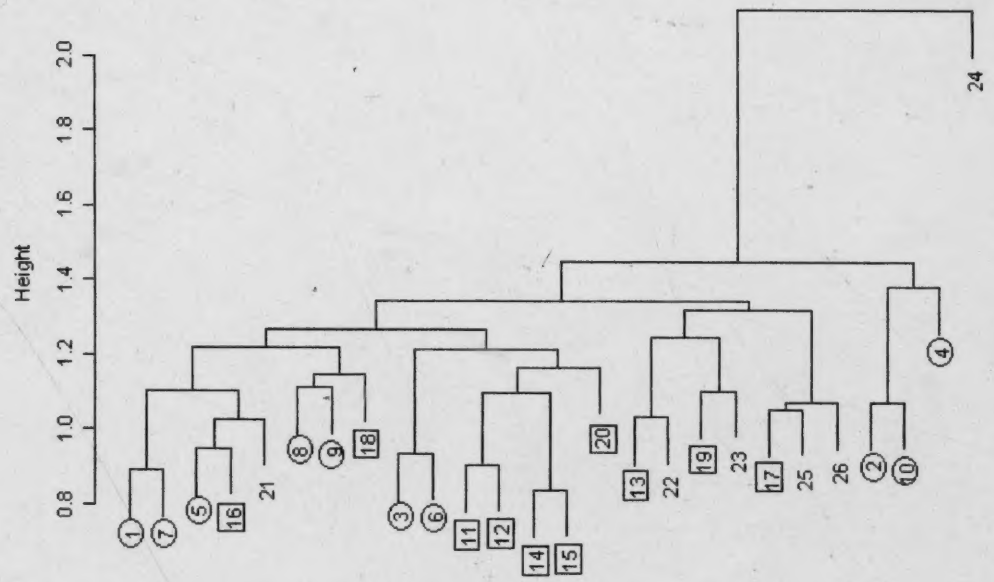



Figure 4.5. Agglomerative hierarchical cluster analysis using the agnes-algorithm in S+ on a matrix of Jaccard similarity coefficients (similarity in species composition) between the plots of all stages together. Circles represent early plots, squares represent intermediate plots and no symbols represent late plots.

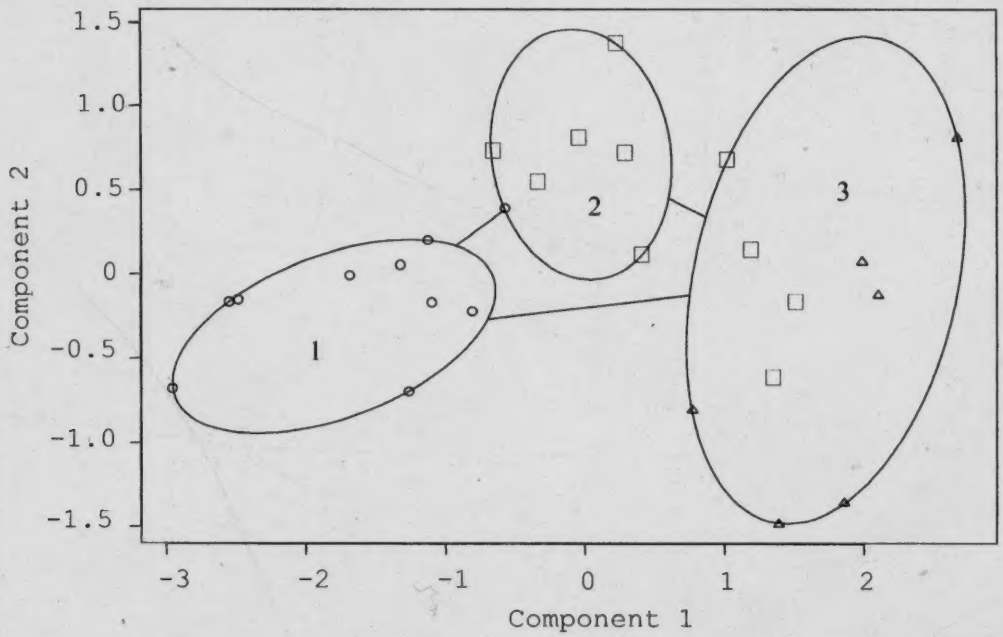



Figure 4.6. Fuzzy partitioning analysis with the fanny algorithm in S+ (into three clusters) of structural variables (H, $G_b$, $S_p$). Ellipses represent the closest hard clustering where 1 is early, 2 is intermediate and 3 late. Circles represent early sites, squares represent intermediate sites and triangles represent late sites.

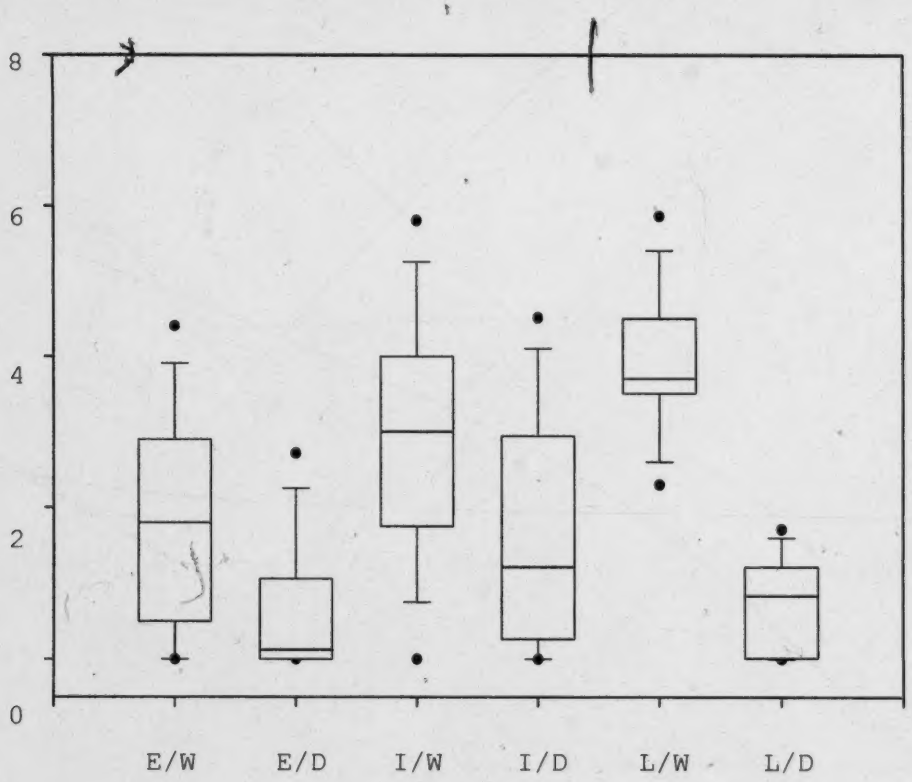



Figure 4.7. Box plots for leaf area index values for the three successional stages during the two extreme seasons. E = early, I = intermediate, L = late, W = wet, D = dry. The boundaries of the boxes indicate the 25$^{th}$ and 75$^{th}$ percentiles. The whiskers above and below the boxs indicate the 90th and 10th percentiles and the dots the 5$^{th}$ and 95$^{th}$ percentile outliers. The median is indicated by a solid line.

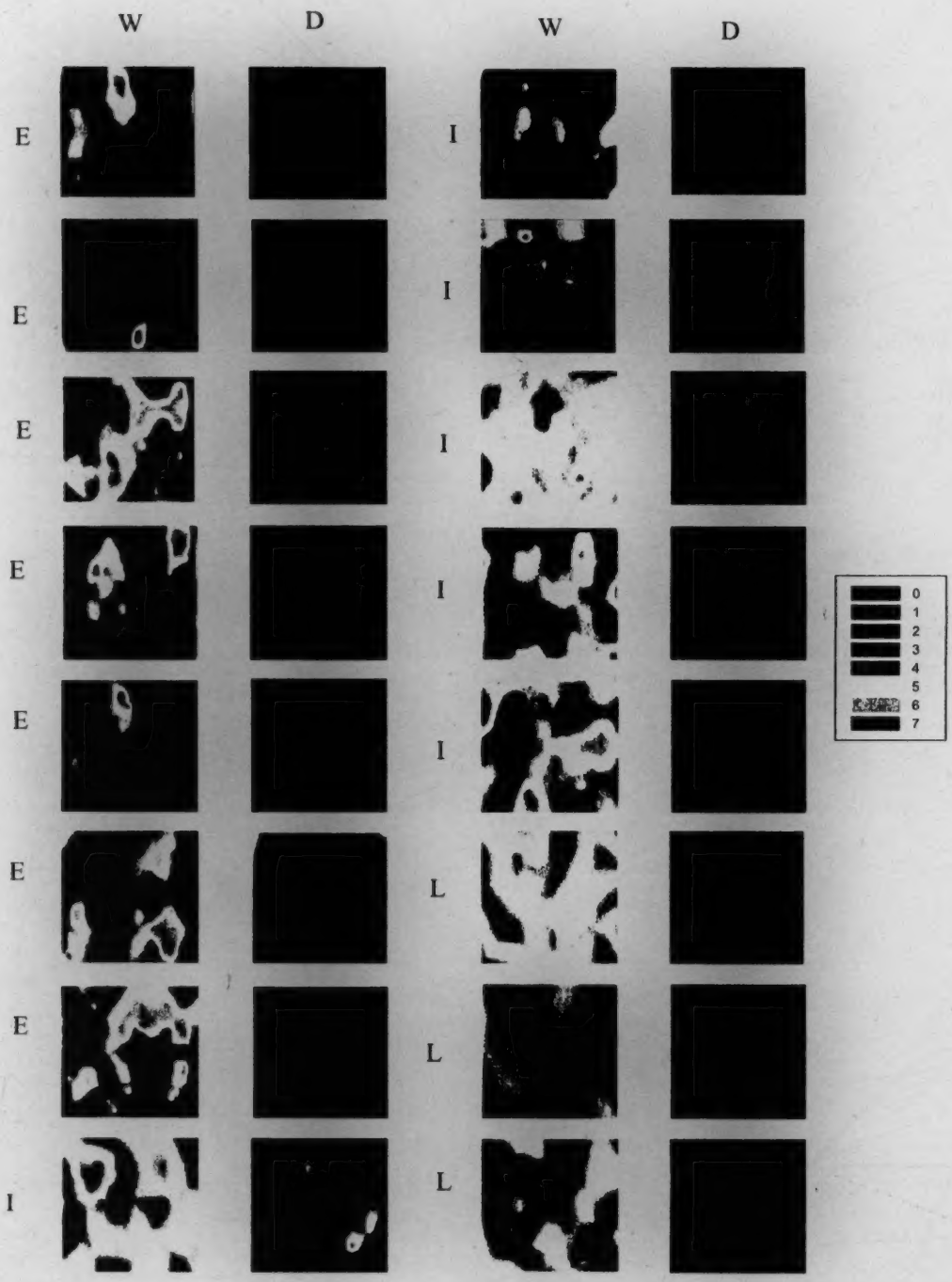
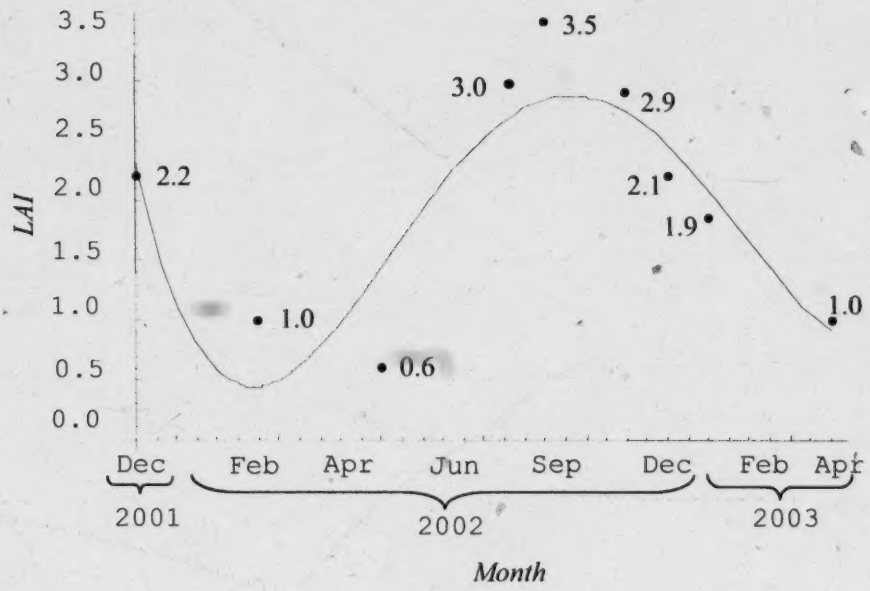
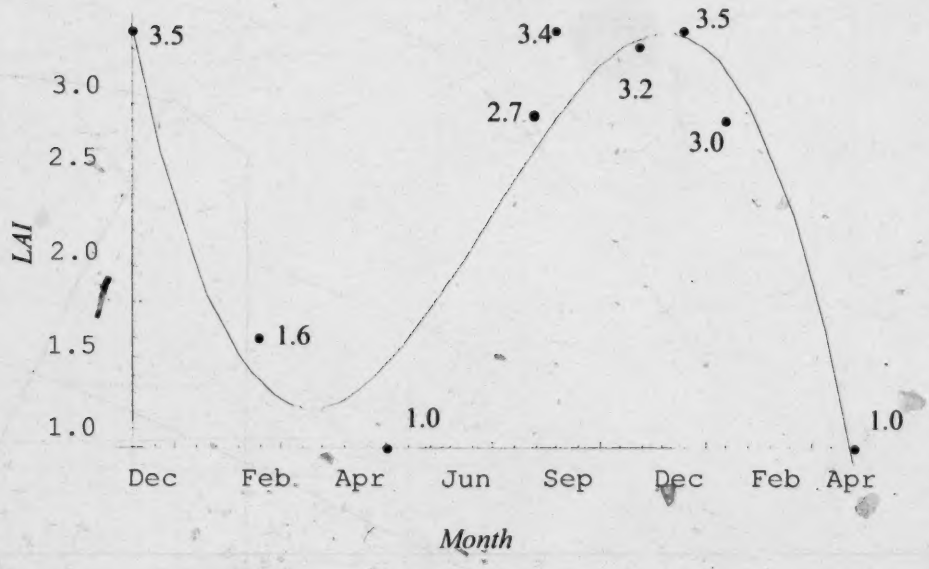

W
D
W
D
E
E
E
E
E
E
E
I
I
I
I
I
L
L
0
1
2
3
4
5
6
7

Figure 4. 8 Contour plots of leaf area index of the three successional stages; early (E), intermediate (I) and late (L) in the wet (W) and dry seasons (D) from Santa Rosa National Park, Costa Rica.

a)


3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
LAI
2.2
1.0
0.6
3.0
3.5
2.9
2.1
1.9
1.0
Dec
Feb
Apr
Jun
Sep
Dec
Feb
Apr
2001
2002
2003
Month

b)


3.5
3.0
2.5
2.0
1.5
1.0
LAI
3.5
1.6
1.0
2.7
3.4
3.2
3.5
3.0
1.0
Dec
Feb
Apr
Jun
Sep
Dec
Feb
Apr
Month

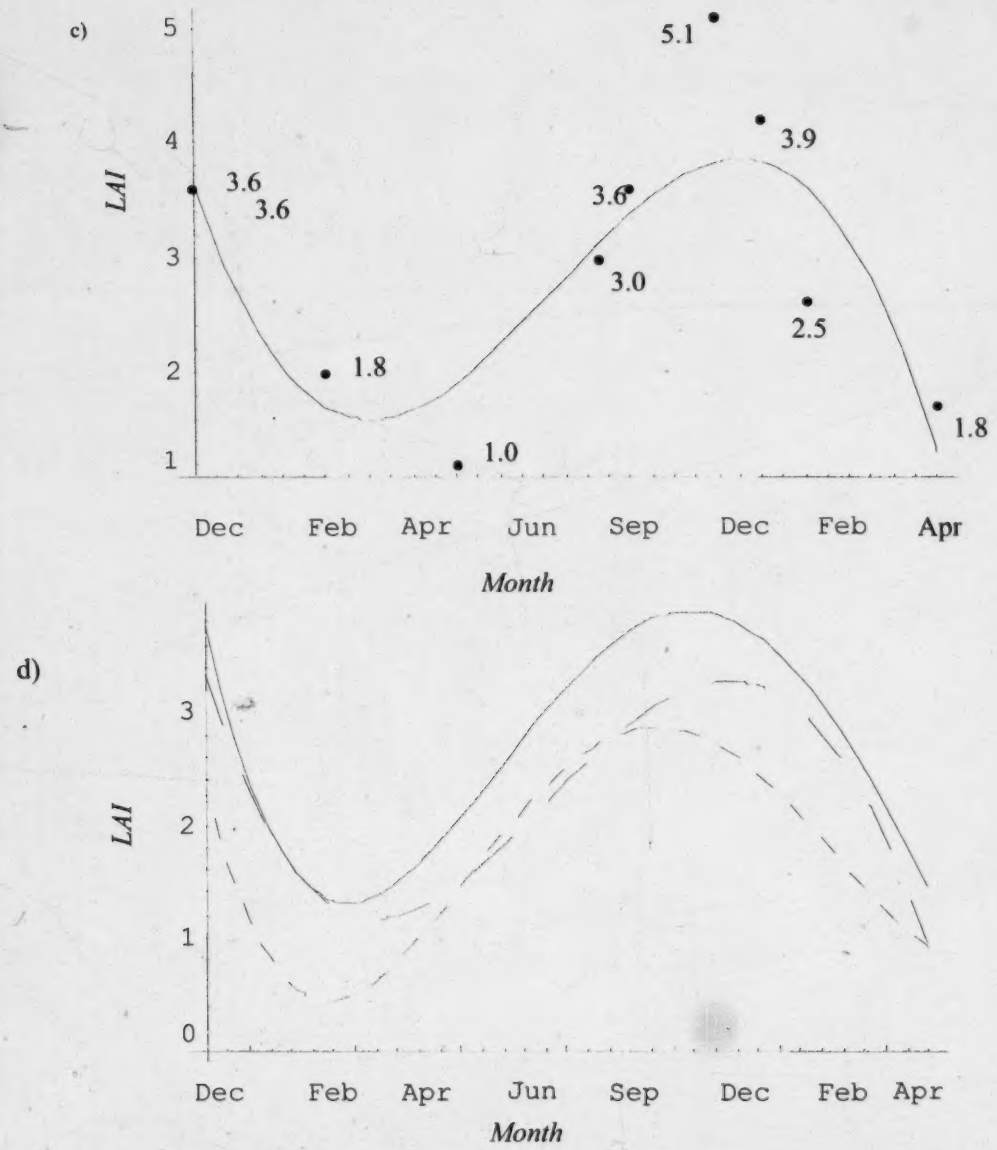
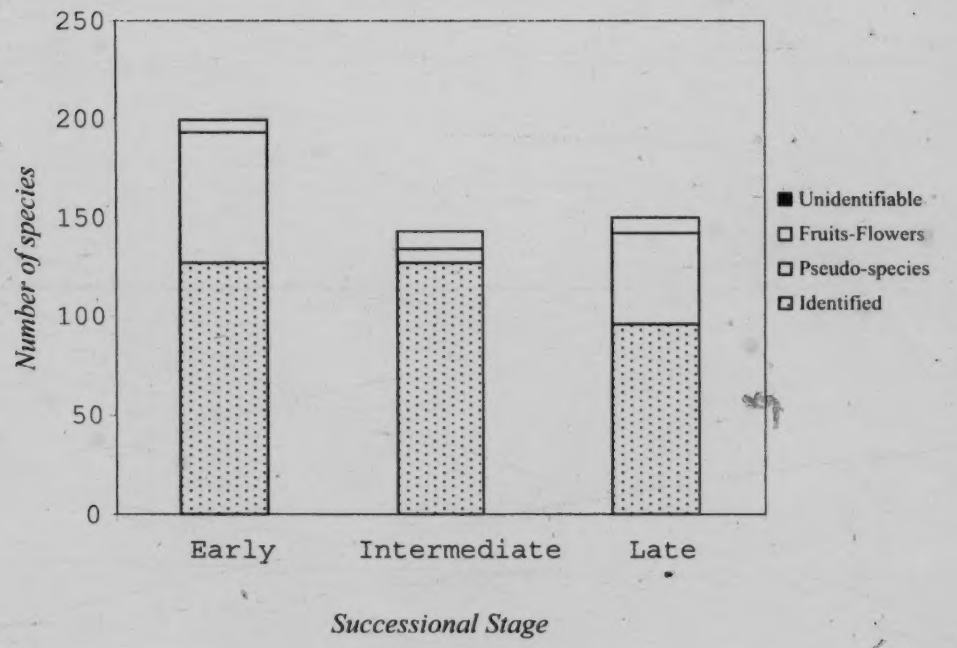
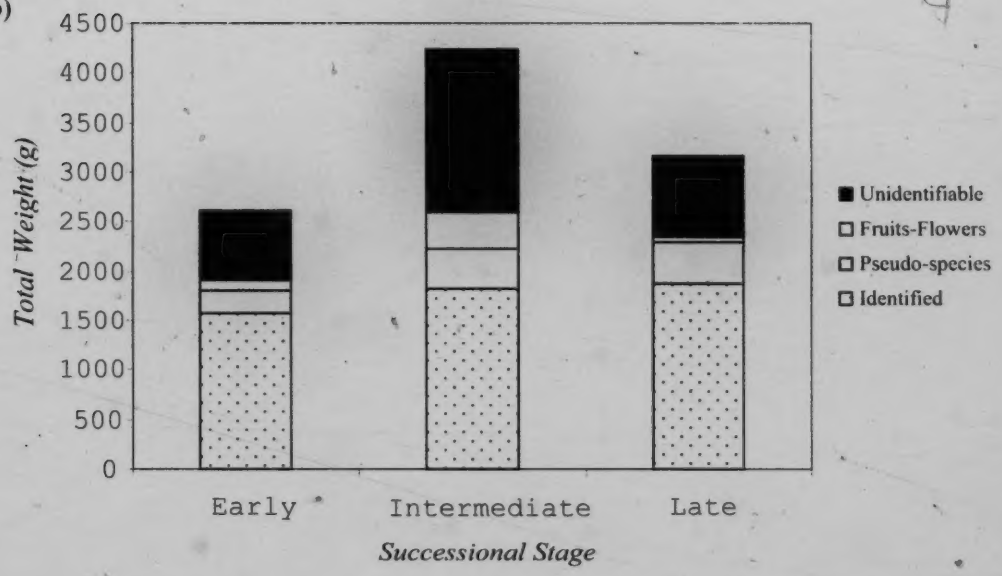


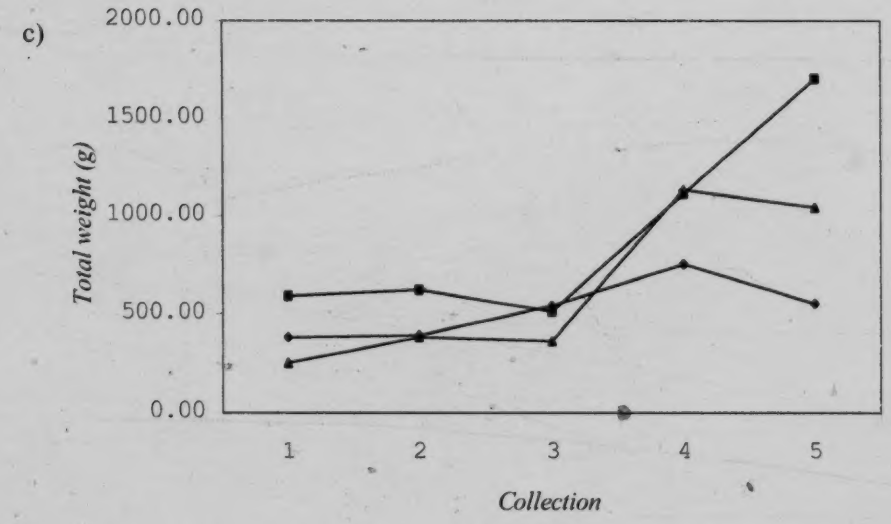

Figure 4.9. Fourth order polynomial function fitted to the leaf area index data of the three stages through the seasons. a) early, b)intermediate c)late and d)means of all three stages where the fine dashes are early, long dashes are intermediate and solid black is late.

a)


250
200
150
100
50
0
Number of species
Unidentifiable
Fruits-Flowers
Pseudo-species
Identified
Early
Intermediate
Late
Successional Stage

b)


4500
4000
3500
3000
2500
2000
1500
1000
500
0
Total Weight (g)
Unidentifiable
Fruits-Flowers
Pseudo-species
Identified
Early
Intermediate
Late
Successional Stage



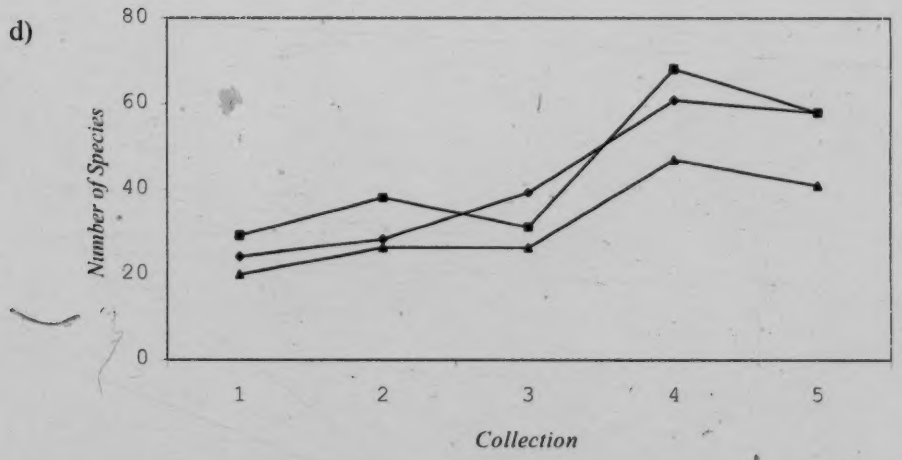




Figure 4.10. a) total number of identified species, pseudo-species and fruits/flowers in each stage from litter traps over five collections. b) total weight of litter collected over five collections. c) total weight collected in the three stages for each collection. d) total number of species collected in in the three stages for each collection. Early stage is represented by diamonds, intermediate by squares and late by triangles.

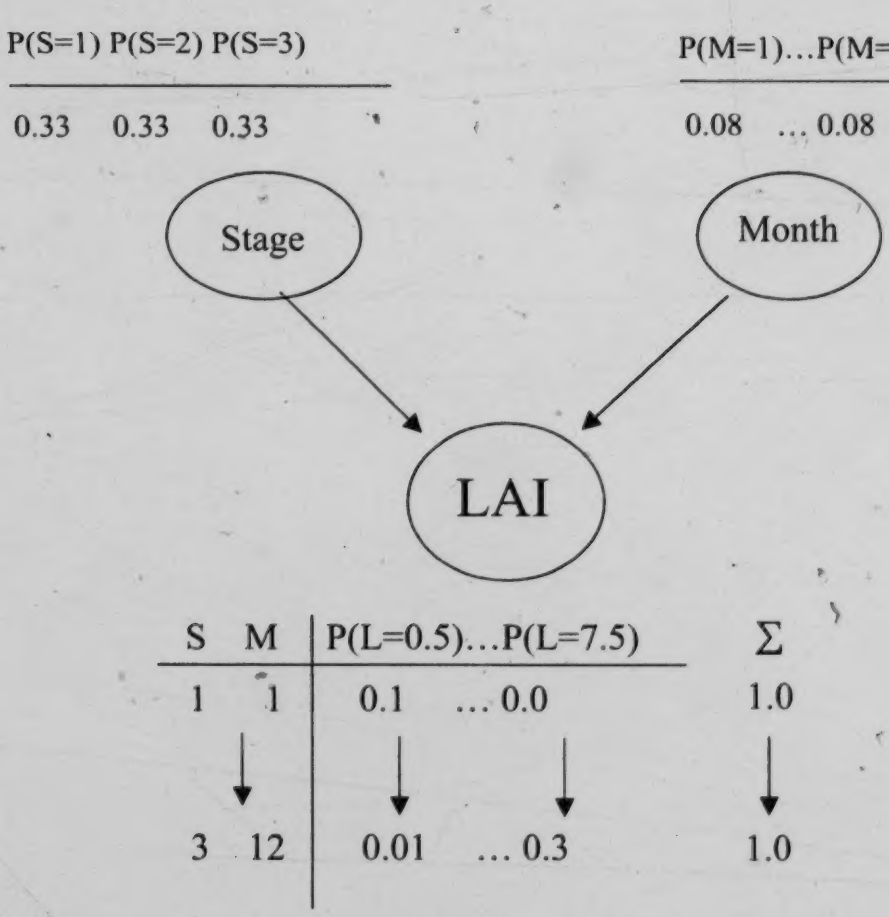



Figure 4.11. Simple Bayesian Network with three nodes. P = Probability, M = Month, S = Stage and L = LAI. Conditional probability tables exhibit the probabilities of each combination of states. For example, the probability of LAI = 0 – 0.5 given that the successional stage is early (1) and it is the month of January (M=1) is 0.1. The probabilities are calculated from the frequency distribution of LAI per stage for each month.

**Appendix A**

In order to assess the applicability of the optical LAI estimates from Santa Rosa to other *T-df* environments, a comparison study is being conducted within the Palo Verde National Park on the Pacific slopes of the Province of Guanacaste (Figure A.1). The park is composed of dry forest along limestone outcrops along with an extensive seasonal wetland region beside the Tempisque River. It is both a Ramsar site and one of the areas with the greatest ecological diversity in Costa Rica. The climate diagram (Walter 1971) for Palo Verde is shown in Figure A.2. It illustrates the seasonality of the precipitation and the length of the dry season.

Using the same methodology as previously described for Santa Rosa in chapter 4, we established 15 30m x 60m plots. Six plots were located in both the early and intermediate successional stages and three in the late (Figure A.1b). The spatial distribution at all scales for the 15 sites was tested using Ripley' K function (Ripley 1976). Our results indicate that all plots (Figure A.3) have a random spatial distribution at scales between 0 and 4000m.

In April 2003, according to the sampling scheme described in chapter 3, we collected optical LAI measurements using the LI-COR 2000 (PCA) in all plots. In addition, in a 20 x 50m subset of each plot we identified and measured the diameter of each woody stem with a DBH great than 5cm. As a comparison, we used the LAI collected with the same methodology (for Chapter 4) in Santa Rosa for April 2003.

*A.2 Results*

The mean and standard deviation of the LAI measurements for each stage is listed in Table A.1. The measurements collected during the first week of April 2003 in Santa Rosa are also listed in Table A.1 for a comparison along with the P value for the D'Agostino-Person test for departure from normality. Only the LAI data from the late stage in both Palo Verde and Santa Rosa have a normal distribution ($P = 0.101$ for Palo Verde and $P = 0.367$ for Santa Rosa). Our results from a Kruskal-Wallis test showed that both in Palo Verde and Santa Rosa there is a significant gradient of LAI through the stages ($P<0.001$). Figure A.4 illustrates the LAI data in the form of box plots for the three stages in both Parks. For Palo Verde, a Mann-Whitney test found significant differences between the LAI values of the early and intermediate stages ($P<0.001$), and the early and late stages ($P<0.001$). However, there was no difference between the intermediate and late stages ($P = 0.489$). For Santa Rosa, the Mann-Whitney test found a difference between the early and intermediate stages ($P = 0.034$), the intermediate and late stages ($P <0.001$) and early and late stages ($P<0.001$). In addition in pair wise comparisons between the same successional stages of the two Parks, we found significant differences for each stage ($P<0.001$ in each case).

*A.3 Discussion*

The same pattern of increasing LAI with each subsequent successional stage is apparent in both Palo Verde and Santa Rosa National Parks. However, while all the stages are significantly different from each other in Santa Rosa, in Palo Verde, the intermediate stage is indistinguishable from the late stage. For all

of the stages the data from Palo Verde is more constrained (i.e. smaller standard deviation, σ) (Table A.1). The greatest difference is in the late stage where the value of the standard deviation for Palo Verde is 0.42 and for Santa Rosa 1.04. In Palo Verde, the early stage is the least dispersed ($\sigma = 0.26$) whereas in Santa Rosa it is the intermediate stage ($\sigma = 0.66$). The maximum LAI value (from the intermediate stage) in Palo Verde is 1.3 and 3.6 in Santa Rosa (late stage). The three main reasons for the difference in LAI values between the two parks are 1) fewer lianas in Palo Verde, therefore when the canopy lost its leaves there isn't the additional woody matter to contribute to optical LAI values 2) not only are the successional stages asynchronous in their leaf phenology (Chapter 4), but so are the two Parks. April was the time of the year with the greatest portion of the canopy being leafless in Palo Verde. In Santa Rosa however, the minimum values for LAI are in February – March (Chapter 4). The second point is important to take into consideration if regional models are being made. This study showed that in even a relatively short geographical distance (65km), two areas of the same ecosystem (*T-df*) have a different timing for leaf phenology. It will be important to continue this comparison in the wet season with the leaves on in order to understand how the pattern changes between the two Parks as well as to documents the changes in LAI from the dry to the wet season in Palo Verde.

Because the main attraction of the station is the fresh water marsh the large expanse of forest is neglected in comparison. Throughout the history of the Palo Verde research station operated by the Organization for Tropical Studies (OTS), the more popular wet forest stations such as La Selva have overshadowed

it. The inclusion of Palo Verde in this study will bring renewed interest to the park and in addition, highlights the differences variable climate and site conditions (i.e. soil, topography) cause in the expression of the forest structural characteristics and leaf area index.

Table A.1 Mean (μ), standard deviation (σ ) and D'Agostino-Pearson test for departure from normality (D'A.P.) P values of optical LAI estimates from Palo Verde and Santa Rosa National Parks.

| Stage | PV - μ | PV - σ | SR- μ | SR- σ | PV - D'A.P | SR – D'A.P. |
|---|---|---|---|---|---|---|
| Early | 0.18 | 0.26 | 0.91 | 0.89 | <0.001 | <0.001 |
| Intermediate | 0.45 | 0.34 | 0.96 | 0.66 | <0.001 | <0.001 |
| Late | 0.50 | 0.42 | 1.74 | 1.04 | 0.100 | 0.367 |

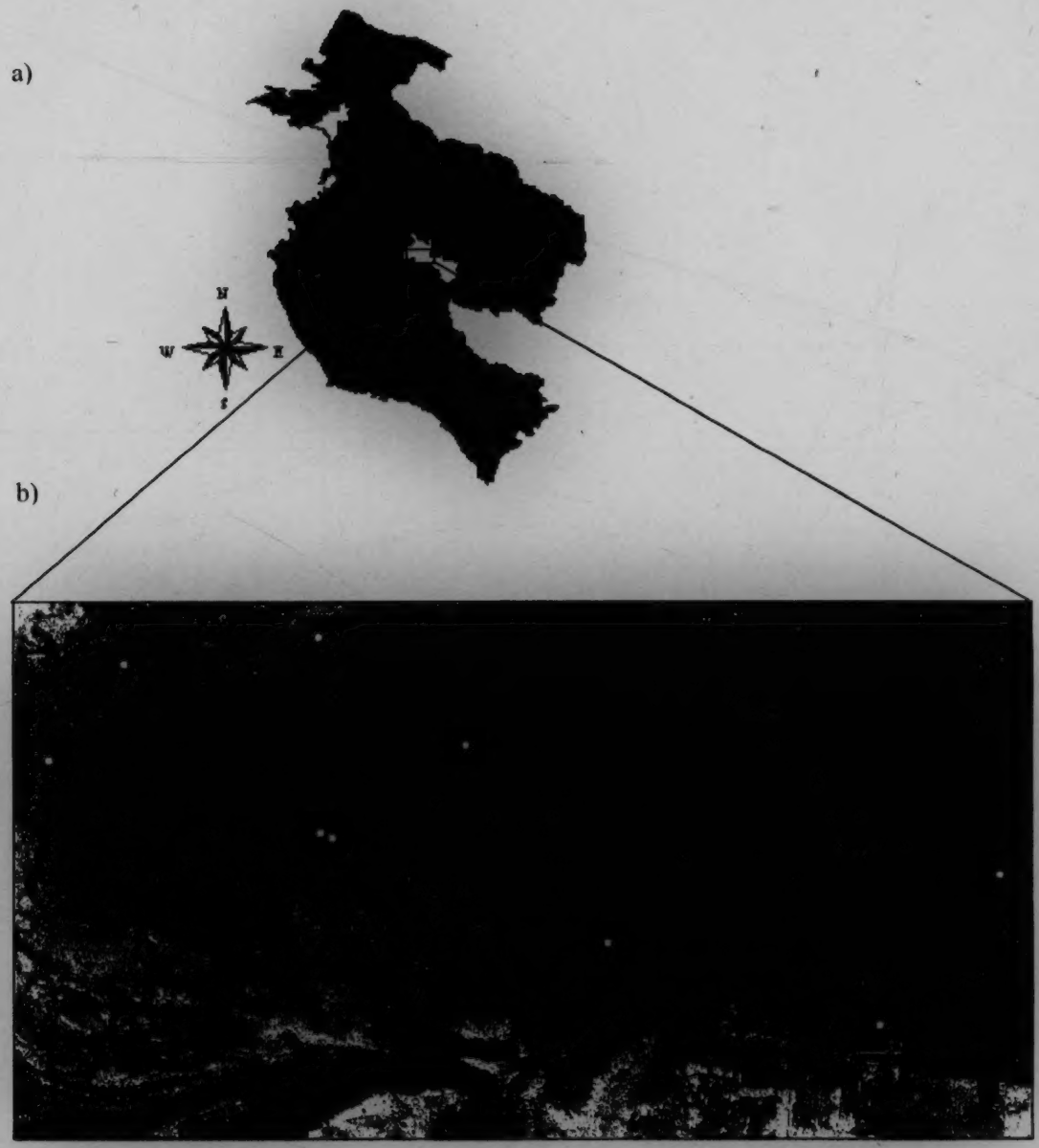



Figure A.1. a) Palo Verde National Park (yellow) with Santa Rosa National Park (white) as a reference in the Chorotega region (dark green) of Costa Rica. b) Plot locations within Palo Verde National Park, early (blue), intermediate (pink) and late (yellow).

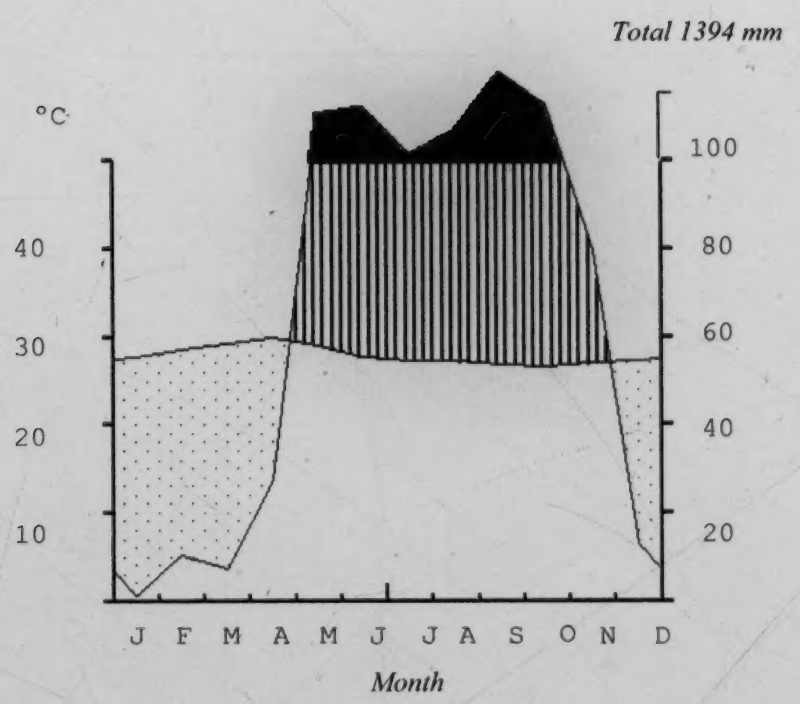



Figure A. 2: Climate diagram for Palo Verde National Park. The mean monthly temperature (°C) and the monthly precipitation (mm) are scaled to represent the potential evapotranspiration. Dry months are represented by the dotted areas, humid months by the vertical lines and months with rain in excess of 100mm are in solid black. Diagram created with ECD, Haase 2000.

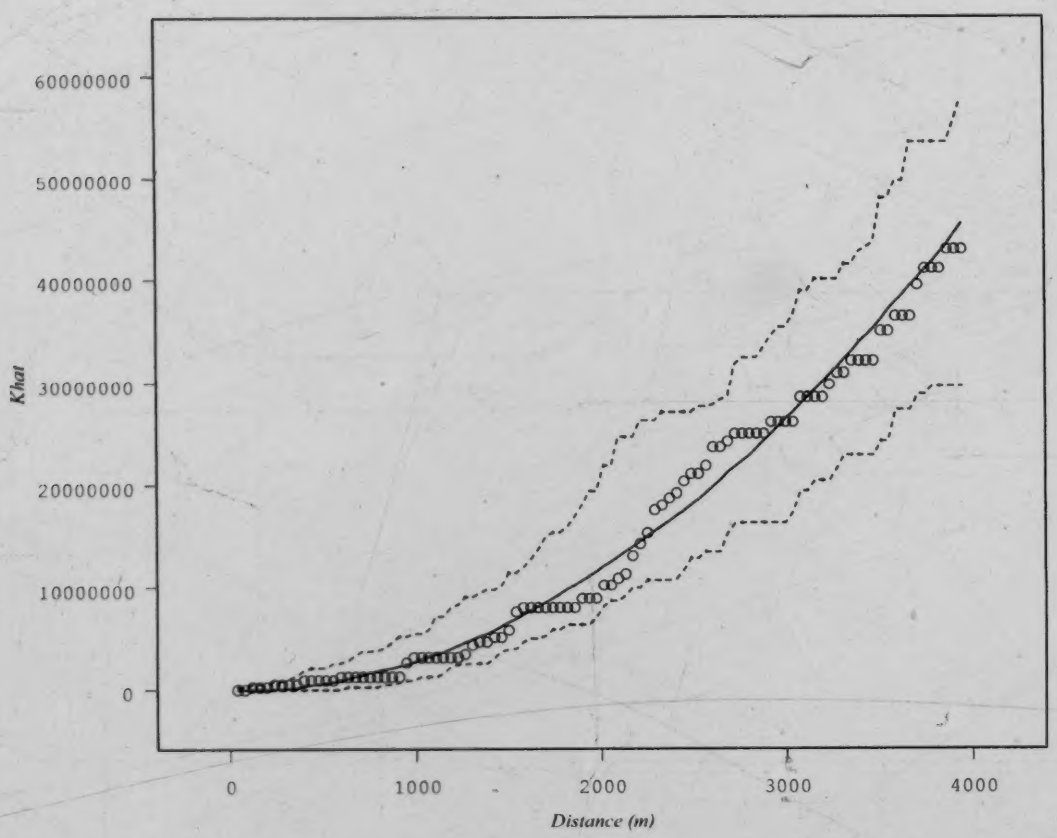



Figure A. 3. Ripley's K function for a spatial point pattern. Solid line indicates the mean for a random distribution, dashed lines indicate the 95% confidence intervals. Open circles represent each of the 100 scales simulated.

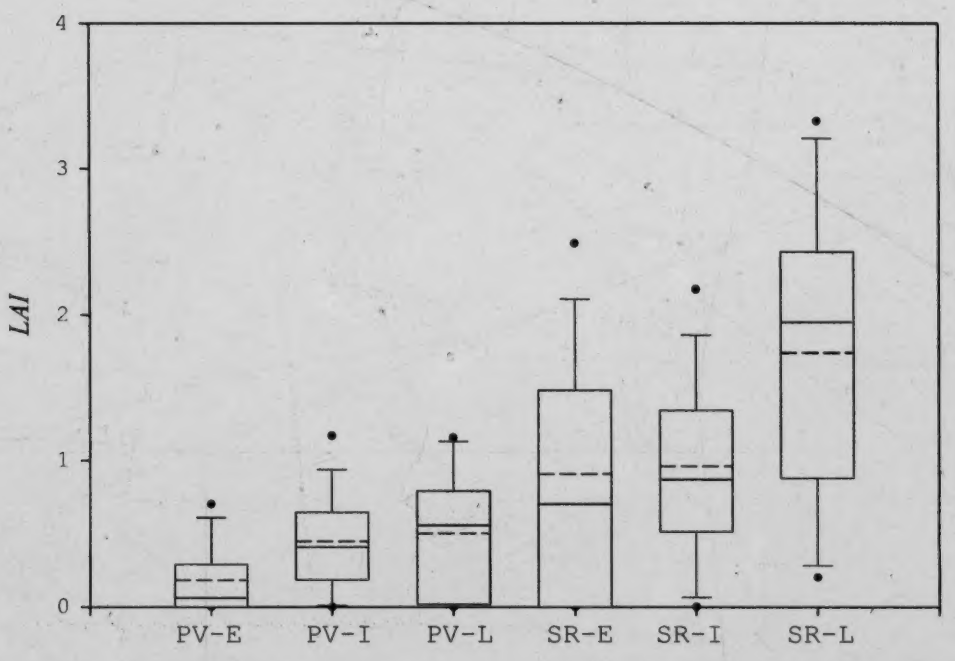



Figure A.4. Optical LAI estimations from April 2003 in Palo Verde National Park (PV) and Santa Rosa National Park (SR) for the three successional stages: early (E), intermediate (I) and late (L). The boundaries of the boxes indicate the 25$^{th}$ and 75$^{th}$ percentiles. The whiskers above and below the boxes indicate the 90th and 10th percentiles and the dots the 5$^{th}$ and 95$^{th}$ percentile outliers. The median is indicated by a solid line and the mean by the dashed line.